BIOMASS PRODUCTION IN AGROFORESTRY TREES AS INFLUENCED BY CUTTING FREQUENCY AND RESERVE CARBOHYDRATES

By

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The relationship between cutting frequency, reserve carbohydrates, and biomass production was examined in *Gliricidia sepium* and *Leucaena leucocephala* in the seasonally dry climate of Ibadan, Nigeria. In the most frequently cut treatment, gliricidia was cut twelve times in 11 months and leucaena was cut eleven times in ten months, at 25 cm above ground level. Sample cores from large roots and lower stems were analyzed for sugars, starch, and total reserve carbohydrates (sugar + starch) using the perchloric acid/anthrone method.

Frequent cutting progressively decreased starch and total reserve carbohydrates. In frequently cut trees, on the last sampling date, starch concentrations in leucaena stems and roots, and gliricidia stems were generally less than 10 % of control values. Starch in gliricidia roots was

approximately 60 % of the control value. In frequently cut trees, sugars in roots and stems were maintained at, or above, control levels throughout the study period. Mortality occurred only in leucaena, after starch in stems and roots had decreased to 2 mg g^{-1} or less.

During shoot regrowth after cutting, starch levels decreased first in stems and, after additional cuts, in roots. Dry-season cuts had little effect on reserve carbohydrates in gliricidia, but quickly reduced stem starch in leucaena.

No starch replenishment occurred during the six weeks after cutting. Following a cut at the end of the dry season, starch reserves in leucaena were substantially restored after three months. In gliricidia, stem starch after seven months was still 50% of the control; root starch was little affected by this cut.

Frequent cutting reduced dry matter production. Generally, there were strong positive correlations between dry matter production, and stem and root starch levels, suggesting that reduced carbohydrate levels contributed to lower biomass production.

A second study evaluated seasonal carbohydrate trends in uncut, 12-year-old trees, including gliricidia, leucaena, *Dactyladenia barteri*, *Pterocarpus soyauxii*, and *Senna siamea*. Sugar and total reserve carbohydrates were highest during the dry season. Starch had two maxima: early in the

dry season and early in the wet season. Lowest starch and total reserve carbohydrate concentrations occurred 2½ to 4 months after the rains began. For maximum biomass production, this would probably be the worst time to cut.

CHAPTER 1
PROBLEM STATEMENT AND OBJECTIVES

As pressure on agricultural land has intensified, it has become increasingly important to investigate alternative agricultural systems which supply necessary products without degradation of the land's productivity. This need is especially critical in humid and subhumid tropical areas that are dominated by low-activity clay soils. Under continuous cropping, these soils quickly lose fertility unless fallow periods—or management practices that provide the benefits of fallow periods—are imposed (Kang et al., 1990; Kang, 1993).

Agroforestry systems, such as alley cropping, can play an important role in such regions. Numerous studies have demonstrated the potential of agroforestry systems for maintaining soil fertility in the humid and subhumid tropics, while meeting the production needs of farmers (Kang et al., 1990; Nair, 1990; Nair, 1993).

Many of the benefits of agroforestry systems are dependent on the ability of trees to coppice vigorously after being cut or pruned. Several studies have demonstrated that increased frequency of cutting decreases subsequent biomass production in woody species used in

tropical alley cropping systems (Guevarra et al., 1978; Osman, 1981; Duguma et al., 1988; Ella et al., 1989). However, few studies have examined the underlying physiological bases of the reduced yields. One possibility is that frequent cutting progressively reduces carbohydrate reserves in the cut plants. Each time foliage and green shoots are removed, the tree must mobilize reserve carbohydrates to rebuild photosynthetic tissue. If cutting cycles are too short, the carbohydrate reserves will not be replenished between cuts.

A four-month study at the International Institute of Tropical Agriculture (IITA) in Nigeria demonstrated that *Gliricidia sepium* uses stem starch to support initial coppice shoot growth after cutting (Erdmann et al., 1993). This study found no correlation between nonstructural carbohydrate concentrations and post-cutting biomass production, but the duration of the study may have been too short for a clear relationship to emerge. A number of researchers—mostly in temperate regions—have correlated low levels of reserve carbohydrates with reduced sprouting ability and reduced initial growth of cut or burned plants (Trlica and Cook, 1971; Miyanishi and Kellman, 1986; Kays and Canham, 1991). More data from tropical areas are required.

If, as seems probable, biomass production in trees is affected by reserve carbohydrate levels, it is important to

know the seasonal cycles of reserve carbohydrates in order to determine the best time to cut to achieve a given objective. Most studies on seasonal cycles have focused on temperate-zone plants. Many trees growing in the tropics exhibit periodicity of growth, especially in areas of seasonal climatic change (Huxley and Van Eck, 1974; Huxley, 1983). However, reserve carbohydrate cycles in these plants have rarely been examined.

Thus, it is clear that there is a shortage of available information on (1) the effect of frequent cutting on reserve carbohydrates in tropical trees; (2) the relationship between cutting frequency, reserve carbohydrate concentrations, and post-cutting biomass production in agroforestry trees; and (3) seasonal reserve carbohydrate cycles in tropical trees, particularly the multipurpose trees used in agroforestry. Increased understanding of these topics will contribute to more efficient and productive management of trees in agroforestry systems, and thus provide greater benefits to farmers and other land managers.

The present study was undertaken to address these issues, with the following objectives:

(1) To determine the effect of different cutting frequencies on reserve carbohydrates in the stems and large roots of *Gliricidia sepium* and *Leucaena leucocephala*.

(2) To examine the relationship between biomass production

and reserve carbohydrate concentrations in periodically cut *Gliricidia sepium* and *Leucaena leucocephala* trees.

(3) To determine the seasonal reserve carbohydrate cycles in the lower boles and structural roots of five tropical multipurpose tree species during a one-year period.

CHAPTER 2
LITERATURE REVIEW

Carbohydrates are the first product of photosynthesis, the chief constituents of plant dry matter, and the substrate for respiration (Kozlowski et al., 1991). Additionally, they are the main energy storage compounds in plants. The term storage has often been used ambiguously. Therefore, Kozlowski (1992) took care to apply this term only to carbohydrates that accumulate in plants and can later be mobilized to support biosynthesis for metabolism and growth. Stored, or reserve, carbohydrates accumulate in woody plants during periods of excess production and are depleted when the rate of carbohydrate utilization exceeds the rate of production (Oliveira & Priestly, 1988; Kozlowski et al., 1991).

In his review of carbohydrate sources and sinks in woody plants, Kozlowski (1992) identified five areas in which reserve carbohydrates play an essential role: respiration, growth, development of cold hardiness, defense against herbivores, and postponement or prevention of mortality. Of particular importance to the present study is the contribution of reserve carbohydrates to vegetative growth. Reserve carbohydrates are known to support regrowth

after cutting or defoliation (Parker & Houston, 1971; Wargo et al., 1972; Gregory & Wargo, 1986; Mika, 1986; Kays & Canham, 1991; Erdmann et al., 1993; Rodgers et al., 1995), resprouting after fire (Miyanishi & Kellman, 1986; Ahrens, 1989; Pate et al., 1990), and early season growth in deciduous trees (Priestly, 1970; Hansen, 1977; Loescher et al., 1990).

Reserve Carbohydrates in Woody Plants

Although plants contain a wide range of soluble and insoluble storage carbohydrates (Lewis, 1984; Loescher et al., 1990), starch is the most prevalent and abundant storage carbohydrate in woody tissues (Kramer & Kozlowski, 1979; Tromp, 1983; Keller & Loescher, 1989). Starch is an insoluble homopolymer of glucose, and occurs within cells as granules in membrane-bound organelles, the plastids (Lewis, 1984). Starch accumulates whenever a high level of sugars builds up, and is transformed to sugars whenever sugars are low in amount (Kozlowski & Keller, 1966).

Of the soluble carbohydrates, sucrose is the principal transportable carbohydrate and the main storage sugar (ap Rees, 1984). Together with starch, it is a major reserve carbohydrate (Kramer & Kozlowski, 1979). Sucrose is a disaccharide formed by the combination of glucose and fructose, and is generally assumed to be stored in vacuoles (ap Rees, 1984). It is found throughout plants, often in

high concentrations (Lewis, 1984). By virtue of its non-reducing nature, it can be translocated and stored without being readily metabolized until required (Arnold, 1968).

Dependent on metabolic activity or environmental conditions, reserve carbohydrates are readily converted from one form to another (Tromp, 1983; Kramer & Kozlowski, 1979). For example, starch-sucrose conversions commonly occur in both vegetative and reproductive tissues (Kramer & Kozlowski, 1979). Because of these frequent interconversions, some researchers believe that it is not necessary to focus too much attention on which particular reserve carbohydrate is most important (Menke & Trlica, 1981; Tromp, 1983). On the other hand, starch—because its deposition and use are affected by sugar levels—often has been used as the sole indicator of the carbohydrate status of woody plants (Ford & Deans, 1977; Adams et al., 1986).

Storage Sites for Reserve Carbohydrates in Woody Plants

The whole tree may be considered a storage organ, with reserve carbohydrates commonly occurring in all perennial parts (Loescher et al. 1990). It has often been noted, however, that the highest concentrations of reserves are usually located in the roots (Priestley, 1964; Kandiah, 1971; Trlica & Cook, 1971; Kramer & Kozlowski, 1979; Menke & Trlica, 1981; Abusrewil et al., 1983; Gregory & Wargo, 1986; Bonicel et al., 1987; Cranswick et al., 1987; Keller &

Loescher, 1989; Loescher et al., 1990; Nguyen et al., 1990; Erdmann et al., 1993). Despite this, the root system should not be regarded as a special storage organ (Priestley, 1960; Tromp, 1983). Kramer and Kozlowski (1979) note that high concentrations may occur in tissues that comprise a low proportion of a plant's total dry weight. In adult trees, for example, the aboveground parts (despite possibly having lower carbohydrate concentrations than roots) may comprise the primary carbohydrate reservoir because they make up a greater proportion of a tree's total dry weight than do roots.

The amount and concentration of nonstructural carbohydrates in the xylem vary with the age and location of the sampled tissues. In sugar maple (*Acer saccharum*), carbohydrate concentrations were about twice as high in the outer sapwood as in the inner sapwood (Murneek, 1942). A study in Nigeria on *Antiaris africana* found that the greatest amounts of nonstructural carbohydrates were stored in the youngest xylem, and concentrations gradually decreased toward the inner sapwood (Olofinboba, 1969). A similar trend was noted in *Pinus sylvestris* (Saranpää & Höll, 1989). In sweet cherry (*Prunus avium*) it was found that one- to three-year-old xylem rings can serve for nonstructural carbohydrate storage but older rings do not (Keller & Loescher, 1989).

Carbohydrate concentrations in coarse roots may vary considerably with root size. Wargo (1976) found that starch content in the roots of *Quercus alba* and *Quercus rubra* varied inversely with root diameter. As root diameter decreased, xylem rays were closer together and the proportion of ray tissue (high starch storage tissue) to woody tissue (low starch storage tissue) increased, resulting in a corresponding increase in starch content. In roots (as well as in stems and branches), the living axial and ray parenchyma cells comprise the major accumulation sites for starch (Kramer & Kozlowski, 1979). In contrast to Wargo (1976), McLaughlin et al. (1980) found similar levels of starch in the large and small roots of *Q. alba*.

Reserve Carbohydrate Concentrations in Woody Plants

Carbohydrate concentrations reported for woody plants are influenced by the tissue sampled, methodological differences, plant age, season and phenological condition of plants at the time of sampling, and whether data are based on one sample period or annual means. Values reported for tropical species include:

- *Antiaris africana*, annual mean, trunk xylem starch, ≈32 mg g^{-1} (estimated from published figure) (Olofinboba, 1969);
- *Camellia sinensis*, one growing-season date, stem starch (32 mg g^{-1}), root starch (180 mg g^{-1}) (Selvendran & Selvendran, 1972);

- *Cedrela odorata*, one growing-season date, root starch, 16.9% to 18.4% of dry weight (Rodgers et al., 1995);
- *Gliricidia sepium*, October-December, stem starch (≈34 mg g^{-1}), stem sugar (≈10-22 mg g^{-1}), root starch (100-210 mg g^{-1}), root sugar (≈7-30 mg g^{-1}) (Erdmann, 1991); and
- *Mangifera indica*, seedlings in growth room, stem starch (13.5%), root starch (25.5%) (Whiley et al., 1989).

Representative temperate zone studies have reported:

- *Acer saccharum*: stem starch (13.5 mg g^{-1}), root starch (35.1 mg g^{-1}) (Gregory & Wargo, 1986); root starch (12-14%) (Wargo et al., 1972);
- *Eucalyptus obliqua*: root starch (1.7-5.2%), root sugar (2.2%) (Kile, 1981);
- *Pinus elliottii*: stem starch (< 8 mg g^{-1}), root starch (20-70 mg g^{-1}), stem sugar (7 mg g^{-1}), root sugar (18 mg g^{-1}) (Gholz & Cropper, 1991).
- *Platanus acerifolia*: root starch (≈60-85 mg g^{-1}) and root sugar (≈7-25 mg g^{-1})—estimated from published figures; stem starch (69.4-117.5 mg g^{-1}), stem sugar (8.4-15 mg g^{-1}) (Haddad et al., 1995);
- *Populus*: root starch (5.1-31.5%) (Nguyen et al., 1990);
- *Prunus avium*: root starch (16-27%) (Keller & Loescher, 1989);
- *Quercus alba*: root starch, 0.15 m from root collar (0-6%) (Wargo, 1976); bole starch (1.7%), root starch (3.9%), bole sugar (0.8%), root sugar (2.0%) (McLaughlin et al.,

1980);

- *Quercus rubra*: root starch, at 0.15 m from the root collar (8-13%) (Wargo, 1976).

Seasonal Variation in Reserve Carbohydrates

Deciduous temperate-zone trees tend to follow a general pattern of carbohydrate use and storage. Carbohydrate reserves decrease during rapid spring growth to a minimum in early summer, and then after vegetative growth has slowed or stopped, increase to an autumn peak. During the winter, respiration causes a slight decline, but reserves are still high when growth resumes in the spring (Priestley, 1962; Kozlowski & Keller, 1966; Kramer & Kozlowski, 1979). Numerous examples of this trend are found in the literature, including *Acer saccharum* (Wargo, 1979), *Betula populifolia* (Gibbs, 1940), *Morus alba* (Yamashita, 1990), *Populus* spp. (Bonicel et al., 1987), *Quercus alba* (McLaughlin et al., 1980), and several North American desert range species (Coyne & Cook, 1970). Loescher et al. (1990) cite more than fifty references that characterize seasonal changes in nonstructural carbohydrates in deciduous fruit and nut trees, and vine crops. Carbohydrates in these trees and vines follow the general trend described above. In some cases, the late-summer accumulation of carbohydrates may be interrupted during the period of fruit ripening (Roper et al., 1988).

Seasonal changes are not as pronounced in recurrently flushing or evergreen species. Annual carbohydrate cycles in recurrently flushing species are characterized by depletion of carbohydrates with each growth flush, followed by carbohydrate replacement between flushes (Kramer & Kozlowski, 1979). This has been reported for species such as *Pinus taeda* (Birk & Matson, 1986), *Pinus radiata* (Cranswick et al., 1987), and *Theobroma cacao* (Sleigh et al., 1984). Mooney and Hays (1973) demonstrated the differences in carbohydrate trends in deciduous and evergreen species. Comparing the drought-deciduous *Aesculus californica* and evergreen *Quercus agrifolia*, they found much more variation in the carbohydrate contents of the deciduous species. However, Gholz and Cropper (1991) reported marked seasonality in starch concentrations in all tissues of *Pinus elliottii* in Florida.

Numerous studies have noted the periodicity of plant growth in tropical areas, and have postulated possible environmental cues (Njoku, 1963; Alvim, 1964; Huxley & Van Eck, 1974; Alvim & Alvim, 1978; Bullock & Solis-Magallanes, 1990; Wright, 1991; Murali & Sukumar, 1993; Borchert, 1994; Wright & Van Schaik, 1994). Although irradiance, photoperiod, and temperature have been suggested, rainfall and seasonal water stress are the most frequently proposed environmental triggers for synchronous plant growth in seasonally dry areas. As noted above, seasonality and

phenology markedly affect nonstructural carbohydrate cycles in temperate plants. The same trend would be expected in tropical plants that grow in areas with distinct wet and dry seasons.

The few studies that have examined reserve carbohydrate cycles in tropical trees in seasonally dry areas have found that carbohydrate concentrations are usually highest early in the dry season and decline when new growth resumes at the end of the dry season. Olofinboba (1969) evaluated the influence of season and growth stage on reserve carbohydrates in the xylem of *Antiaris africana* in the Onigambari Forest Reserve near Ibadan, Nigeria. He found that concentrations of the different reserve carbohydrates tended to rise and fall together. Starch and sucrose concentrations peaked at leaf fall, approximately one month after the dry season began, and declined to a minimum when seed production and leaf flush commenced at the end of the dry season. From this low point, carbohydrate concentrations increased, reaching a more or less steady state until the next leaf fall. A study with *Gliricidia sepium* at IITA in Nigeria also found evidence that reserve carbohydrates accumulate early in the dry season (Erdmann et al., 1993). In a Mexican deciduous forest, Morales et al. (1992) found that, in both bark and wood, most tree species had the least amount of starch in late spring and summer (wet season) and the greatest amount during autumn and

winter (dry season). The amount of starch decreased at the beginning of the rainy season, coinciding with the development of new shoots. Similarly, Singh and Srivastava (1986) reported that total nonstructural carbohydrates in the fine roots of *Tectona grandis* in India were at their highest levels two months into the dry season and lowest levels in the early part of the rainy season.

Reserve Carbohydrates and Biomass Production

A number of researchers have reported that the frequency with which multipurpose trees are cut affects subsequent biomass production. Ella et al. (1989) compared yields in four species—*Leucaena leucocephala*, *Gliricidia sepium*, *Sesbania grandiflora*, and *Calliandra calothyrsus*—that were cut at either six-week or twelve-week intervals. The longer cutting interval resulted in higher yields, and this effect was more pronounced for wood yield than for leaf yield. Duguma et al. (1988) cut the first three of the above species at intervals of one, three, or six months and obtained similar results. The same trend was also reported for *L. leucocephala* by Guevarra et al. (1978), Ferraris (1979), and Krishnamurthy and Munegowda (1982). Erdmann et al. (1993) found that cutting *G. sepium* at six-week intervals produced more dry matter than cutting at three-week intervals.

Few studies have investigated the physiological processes that might be influenced by cutting frequency and which might, in turn, affect biomass production. Reserve carbohydrate status might be relevant in this regard. As was described in the preceding section (Seasonal Variation in Reserve Carbohydrates), reserve carbohydrates in woody species follow definite seasonal trends. Carbohydrate reserves tend to decrease considerably during periods of rapid growth, a trend which implies that reserve carbohydrates are mobilized to support the growth.

Similar reductions in reserve carbohydrates have been reported for woody species after defoliation or loss of aboveground parts. As new growth is produced, reserve carbohydrate levels decline. Examples from temperate areas include *Acer saccharum* (Parker & Houston, 1971; Wargo et al., 1972; Gregory & Wargo, 1986), *Morus alba* (Satoh et al., 1977; Yamashita, 1986), *Populus* spp. (Eliasson, 1968; Tschaplinski & Blake, 1994), *Platanus acerifolia* (Haddad et al., 1995), *Quercus* spp. (Parker & Patton, 1975; Parker, 1979), *Pseudotsuga menziesii* (Webb & Karchesy, 1977), *Eucalyptus* spp. (Bamber & Humphreys, 1965; Old et al., 1990), *Prunus avium* (McCamant, 1988), pecan (*Carya illinoensis*) (Worley, 1979), *Citrus* spp. (Eissenstat & Duncan, 1992), and several desert range species (Trlica & Cook, 1971; Buwai & Cook, 1977). The few extant studies on tropical species have reported similar trends. These

include tea (*Camellia sinensis*) (Nagarajah & Pethiyagoda, 1965; Selvendran & Selvendran, 1972; Kandiah et al., 1984), *Cedrela odorata* (Rodgers et al., 1995), *Gliricidia sepium* (Erdmann et al., 1993), and two tropical savanna shrubs—*Clidemia sericea* and *Miconia albicans* (Miyanishi & Kellman, 1986).

Many of the above studies indicated that a plant's reserve carbohydrate status will affect its ability to sprout and produce biomass. The least amount of sprouting and growth, and the highest mortality are associated with low carbohydrate levels (Miyanishi and Kellman, 1986). Therefore, time of cutting and frequency of cutting are important considerations.

Generally, coppice sprouting is most vigorous if trees are cut during the dormant season, whereas it is least vigorous if trees are cut when shoot elongation is rapid (Blake, 1983). The implication from this observation is that vigorous coppice sprouting is correlated with the relatively high concentrations of reserve carbohydrates that occur during the dormant season. During the growing season, reserve carbohydrate levels in deciduous trees at the time of cutting may be less important than levels at the end of the season. In a study of four hardwood species—*Acer rubrum*, *Fraxinus americana*, *Prunus serotina*, and *Betula populifolia*—Kays and Canham (1991) found that there was a well-defined window of time during the growing season when

cutting resulted in low levels of root starch at the end of the growing season, and subsequent low sprout-growth rates the following year. Cutting at the very beginning or very end of the growing season resulted in the highest levels of autumn root reserves and sprout production.

Carbohydrate reserves in roots may be especially important to growth in coppiced plants because aboveground storage sites are removed or reduced. Several radioisotope labeling studies have demonstrated that carbohydrates stored in roots are mobilized to support aboveground growth. In studies with apple (*Malus* spp.) (Quinlan, 1969; Hansen, 1967), pecan (Lockwood & Sparks, 1978), and sweet cherry (McCamant, 1988) ^{14}C that was translocated to roots in autumn was detected in new leaves and shoots the following season. Roots, however, are not the only source of reserve carbohydrates. Carbohydrate sinks generally deplete reserves close to the site of utilization before using more distant reserves (Kramer & Kozlowski, 1979).

Multipurpose Trees

In the agroforestry context, multipurpose trees are understood as "those trees and shrubs which are deliberately kept and managed for more than one preferred use, product, and/or service; the retention or cultivation of these trees is usually economically, but also sometimes ecologically, motivated, in a multiple-output land-use system" (Nair,

1993, p. 172). Five multipurpose tree species were included in the present study: *Dactyladenia barteri*, *Gliricidia sepium*, *Leucaena leucocephala*, *Pterocarpus soyauxii*, and *Senna siamea*. Each is described below.

Dactyladenia (Acioa) barteri (Hook. f. ex Oliv.) Engl. (Chrysobalanaceae)

Dactyladenia barteri is an evergreen shrub or small tree (to 12 m in height) that is indigenous to West Africa, from Zaire to Liberia (Burkill, 1985). Farmers on acid ultisols in southeastern Nigeria have used this species for many generations in a traditional fallow/alley cropping system (Kang et al., 1990). In this system, hedgerows of *Dactyladenia* shrubs that are planted 2-3 m apart provide nutrient cycling, weed suppression, livestock fodder, and staking material. They are pruned prior to a one- to two-year cropping cycle, and then allowed to regrow for two to three years before starting the next cycle. In Nigeria's humid zone, on acid and low-base soils, *D. barteri* is one of the most promising species for alley cropping with cassava and plantain (Kang et al., 1991). According to Ruhigwa et al. (1992), it has very desirable rooting patterns for alley cropping on acid soils.

A recent two-year study that compared the effects of mulches from different sources found that decline in maize grain yield from one year to the next was least with *Dactyladenia* prunings (Tian et al., 1993). Other mulches included in this study were gliricidia and leucaena

prunings, maize (*Zea mays*) stover, and rice (*Oryza sativa*) straw. Mulching with *Dactyladenia* prunings significantly reduced soil temperature, helped conserve soil moisture, and increased nutrient uptake over the control.

Gliricidia sepium (Jacq.) Walp. (Leguminosae-Papilionoidae)

Gliricidia sepium, commonly known as gliricidia, is a medium-sized tree that is native to Mexico and Central America, but now has a pantropical distribution. Hughes (1987) has provided the best description of gliricidia in its native habitat; the background information in this paragraph is drawn from his work. In gliricidia's native range, a subhumid climate prevails with annual rainfall in the range of 900-1500 mm and a five-month dry period from December to April. However, gliricidia can occur on sites with rainfall as low as 600-700 mm and as high as 3500 mm. Gliricidia loses some or all of its leaves during the dry season, and flowers and fruits while leafless. Leaf flush occurs as the last seeds are shed, about one month prior to the first rain. Gliricidia resprouts vigorously after severe fires, which has contributed to its dominance in some areas.

With the exception of leucaena (*L. leucocephala*), gliricidia is believed to be the most widely cultivated multipurpose tree (Simons & Stewart, 1994). It is used to supply products such as fuelwood, poles, staking material, green manure, fodder, and bee forage. Additionally, it is

used for crop shade, live fences, and erosion prevention (Simons & Stewart, 1994).

Long-term observations in the humid/subhumid zones of southwestern Nigeria have shown that at low altitude on high-base soils, gliricidia and leucaena are the two most suitable species for use in alley farming (Kang, 1993). At Ibadan, Nigeria, alley-cropped gliricidia that was pruned five times during a year produced 5.5 t ha^{-1} $year^{-1}$ of leaf and twig dry matter, with a nitrogen content of 169 kg (Juo & Kang, 1989). Yamoah et al. (1986b) reported a similarly large N yield for gliricidia. Only a portion of the potential N yield in biomass that is returned to the alleys is actually taken up by associated crops. Kang (1987) estimated that the effective N contribution from gliricidia and leucaena hedgerows to alley-cropped maize was about 40 kg N ha^{-1}. In trials in Ibadan and Oyo, Nigeria, maize in gliricidia or leucaena alley farming systems was given 0, 40, or 80 kg N ha^{-1} and mulched with 0, 50, or 100% of the hedgerow prunings; maize grain yields increased with increasing levels of mulch, and increased with higher N rates, even at the highest level of mulching. Soil organic carbon, N, and available P also tended to increase with increasing levels of mulch (Larbi et al., 1993).

Leucaena leucocephala (Lam.) de Wit (Leguminosae-Mimosoideae)

Leucaena leucocephala, commonly known as leucaena, is probably the most widely grown tree legume in the world (Bray, 1994). It is native to the Central American lowlands but now has a pantropical distribution (Pound & Martinez Cairo, 1983). Unless otherwise noted, the following background information is based on NAS (1984).

The numerous varieties of leucaena have been classified into three groups according to size and growth habit. The trees included in the present study belong to the "giant type." Trees in this group grow to 20 m in height, with thick, almost branchless trunks. They flower seasonally, usually twice per year.

Leucaena is normally an evergreen tree but sheds its leaves during prolonged droughts. It grows best where annual rainfall is 1000-3000 mm, but also occurs in dryer areas. Leucaena can survive dry seasons lasting eight months or longer. In dry environments, however, yields are low and are believed to increase linearly from 800 to 1500 mm, other factors being equal (Brewbaker et al., 1985). Leucaena has a deep tap root which contributes to drought tolerance, especially in areas with adequate subsoil moisture. Lateral roots are usually sparse on adult plants.

The various uses of leucaena have been reviewed in a number of publications, including Pound and Martinez Cairo (1983), NAS (1984), and Brewbaker (1987). Leucaena can

supply products such as animal fodder, green mulch, pulp wood, lumber, and fuelwood. In addition, when incorporated into agricultural and forestry systems, it can provide benefits such as soil protection, erosion control, fertility maintenance, crop shade, and wind protection. Because leucaena hedges remain green during the dry season when the risk of fire is high, leucaena is planted in fire breaks around forest plantations. In Nigeria, leucaena has been suggested for use in efforts to reclaim tin minelands for farmers (Phillips-Howard, 1993). [A second species from the present study, *Senna siamea*, was also recommended for this purpose.]

As was mentioned in the gliricidia section, leucaena is one of the best species for use in alley cropping on high-base soils in the humid/subhumid tropics (Kang, 1993). At Ibadan, Nigeria, alley-cropped leucaena that was pruned five times during a year produced 7.4 t ha^{-1} $year^{-1}$ of leaf and twig dry matter, with a nitrogen content of 247 kg (Juo & Kang, 1989). A study which reported beneficial effects of leucaena prunings on maize yields and soil chemical properties (Larbi et al., 1993) was described in the preceding (gliricidia) section. Another study at Ibadan—conducted over a five-year period—found that soil chemical properties were maintained in a leucaena alley-cropping system, whereas in a *Senna siamea* system soil organic matter, N, pH, and CEC declined to levels comparable

with those recorded in a continuous monocropping system (Van Der Meersch et al., 1993). Despite this, maize yield was consistently higher in the *S. siamea* system. It was concluded that leucaena was preferable when organic fertilizers were unavailable, but *S. siamea* was preferable when they were available.

Pterocarpus soyauxii Taub. (Leguminosae-Papilionoidae)

Pterocarpus soyauxii is a rainforest tree that can attain a height of 30 m and a girth of 2.5 m. Its range extends from southwestern Nigeria to Zaire (Keay, 1989). It has been reported that in Nigeria *P. soyauxii* produces flowers in June, September, and October, and fruit from August through January (Keay, 1989). Leaf flushes occur mainly from December through March, but also in October, November, and April (Okigbo, 1977).

In parts of Nigeria, the edible leaves of these trees are an important vegetable during the dry season when conventional annual vegetables are scarce or unavailable (Okigbo, 1977; Okafor, 1979). Leaf shedding occurs during a short period of time, and is followed immediately by a flush that produces large quantities of edible young leaves. This growth pattern makes *P. soyauxii* the preferred species for large-scale production of edible material. Farmers protect the natural regeneration of these trees, and cultivate it to a limited degree in the forest zone. It is abundant in and around compound farms (Okafor, 1979).

P. soyauxii has several other traditional uses in Nigeria. It is frequently protected or grown in sacred groves, and plays a role in traditional religious ceremonies (Okafor, 1979). It is also a source of camwood, which when ground, yields a red dye used for cosmetic purposes in rural areas of several Nigerian states (Okafor, 1979). Red dye extracted from the heartwood is also used extensively in Europe to color foods such as ketchup (NAS, 1979).

Timber from *P. soyauxii* is highly prized and makes excellent furniture wood (NAS, 1979; Ogata, 1989). It is marketed under the names barwood, redwood, Gabon padauk, African coralwood, and African padauk.

<u>*Senna (Cassia) siamea* (Lam.) Irvin & Barley (Leguminosae-Caesalpiniodeae)</u>

Senna siamea is native to Southeast Asia, but has been widely distributed and naturalized in tropical regions around the world (Little, 1983). It flowers and fruits during most seasons, and grows to a height of 20 m (Keay, 1986). Although a legume, *S. siamea* is believed not to be nitrogen fixing. Despite this, it holds large amounts of nitrogen in its foliage and appears capable of improving soil nitrogen (Young, 1989).

In Nigeria, it is commonly cultivated in fuelwood plantations, and as an ornamental and shade tree in and around towns (Keay, 1989). Additionally, it is used in windbreaks and reforestation efforts (Ruhigwa et al., 1993). It is a promising hedgerow species for alley-cropping

systems in the moist subhumid tropics (Yamoah et al., 1986a, 1986b, 1986c), as well as in semiarid regions (Danso & Morgan, 1993; Jama, 1993). It can be grown on neutral to acid soils.

Alley-cropping trials at IITA that included gliricidia, *Flemingia congesta* (also known as *F. macrophylla*), and *S. siamea* found that *S. siamea*: (1) had the greatest potential to control weeds (Yamoah et al., 1986a); (2) produced the highest dry matter yield and the highest amount of wood per hectare (Yamoah et al., 1986b); (3) contributed the most total N per hectare, even though percent leaf N content of *S. siamea* was lower than that of gliricidia, and contributed the highest amounts of P and K at the first pruning (Yamoah et al., 1986b); (4) produced better maize yields than the control (Yamoah et al., 1986b); and (5) reversed soil organic matter decline, improved soil structure, increased soil N, and improved soil P (Yamoah et al., 1986c). In contrast to Yamoah et al. (1986c), Van Der Meersch et al. (1993) did not find improved soil organic matter, N, or CEC under *S. siamea* alley cropping. Perhaps the two-year duration of the former study was too short to detect long-term changes in soil properties.

CHAPTER 3
EFFECTS OF CUTTING FREQUENCY ON RESERVE CARBOHYDRATES AND POST-CUTTING BIOMASS PRODUCTION IN *GLIRICIDIA SEPIUM* (JACQ.) WALP. AND *LEUCAENA LEUCOCEPHALA* (LAM.) DE WIT

Effects of Cutting Frequency on Reserve Carbohydrates and Biomass Production in *Gliricidia Sepium* (Jacq.) Walp.

Materials and Methods

Study site

The study was conducted at the main research station of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria (latitude 7° 30' N and longitude 3° 54' E). This location lies in a zone of transition between the humid and subhumid tropical climates (Moormann et al., 1975). An average annual rainfall of 1100 to 1300 mm is received over two distinct growing seasons—the first from mid-March to mid-July, and the second from mid-August to the end of October (Lal, 1989). The two rainy seasons are separated by a short dry period from mid-July to mid-August, while the major dry season occurs from early November to mid-March. Mean monthly temperatures range from 24° to 28°C, with the highest temperatures occurring towards the end of the long dry season.

Field work for the present study was conducted from December 1991 through December 1992. During this period, IITA received 1,171 mm of rainfall. Figure 1 shows monthly rainfall, relative humidity, and temperature during the study period. Weather during this interval generally conformed to historical patterns, although less than normal rainfall was received during both the long and short dry periods.

Most soils at IITA are Alfisols with an average effective CEC of 6.2 cmol kg^{-1} soil (Moormann et al., 1975). The soil of the experimental plot was classified as an Oxic Paleustalf, and texturally as a sandy clay loam.

Gliricidia seedlings of the local Ibadan variety were planted on the site (A6W) in May of 1985 in an alley cropping configuration. Within-row spacing was 0.5 m and between-row spacing was 4.0 m. The hedges were cut two times per year from 1988 through 1990 at a height of approximately 75 cm. During this three-year period, maize was grown in the alleys during both rainy seasons. Gramoxone (or Paraquat — 1,1′-dimethyl-4,4′-bipyridinium ion) was applied to plots before maize was sown. All prunings from the gliricidia hedgerows were returned to the soil, supplemented by an equal quantity of panicum grass (*Panicum* sp.) prunings. Approximately 45 kg of prunings from each of these plant species were added to each 4 x 4 m plot twice per year during the course of the maize

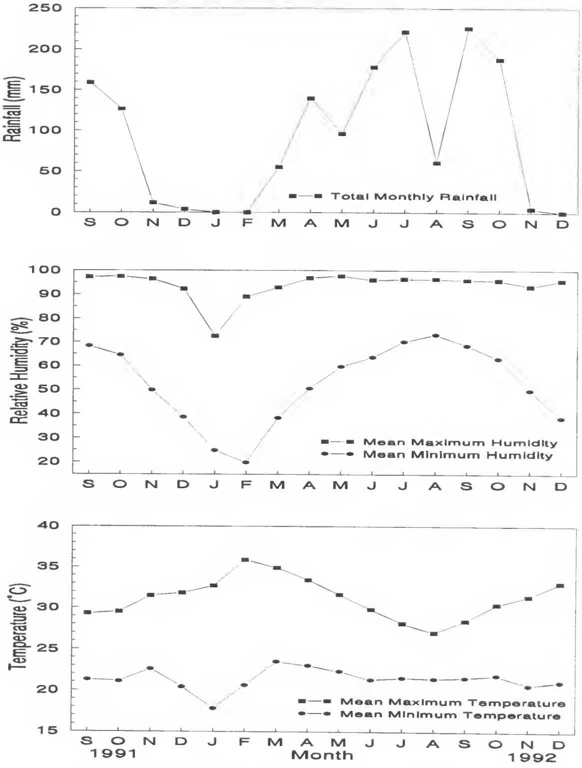

Figure 1. Weather at the International Institute of Tropical Agriculture, Ibadan, Nigeria during the study period.

experiment. In 1990, the site was fertilized with 15 kg N per hectare. After the final 1990 maize harvest, the site was fallowed until the initiation of the present study in December 1991.

Hedgerow trees were six years old and had grown undisturbed for over one year when the cutting-frequency study began. Mean tree height was approximately 5 m, and there was almost complete canopy closure over the alleys. In total, the study included 928 m of hedgerows and encompassed an area of approximately 0.37 hectares.

At the beginning of the experiment, the alleys between hedgerows were heavily overgrown with weeds, vines and, especially, panicum grass. Alleys were manually cleared with cutlasses (machetes), and were kept clear in this manner for the duration of the experiment. It was necessary to apply gramoxone twice (May 8, 1992 and June 24, 1992) in order to control the panicum grass.

Experimental design and sampling procedure

The study was set up as a randomized complete block with 5 blocks, 4 treatments, and 34 trees per plot (distributed over 4 hedgerows). Buffer areas were located between treatments containing tall plants and those containing more frequently pruned plants in order to minimize the effect of shading. Trees in buffers were pruned along with other trees in a plot but were not sampled or included in biomass estimates. Treatments consisted of:

(1) uncut control;

(2) seasonal cutting--cut at the start of the study, the end of the long dry season (March), the end of the rainy season (October), and on the last sampling date;

(3) cut at 6-week intervals;

(4) cut at 6-week intervals during the dry season (December to March), and otherwise at 3-week intervals.

Trees in treatments 2, 3, and 4 were initially cut during the period of December 10-13, 1991. At this time, a chainsaw was used to cut all trees to within 25 cm of the ground. During subsequent cuttings, all coppice sprouts were cut to within 1 cm of the stump. Care was taken to remove all green biomass, so that only woody biomass remained. Including the initial and final (December 1992) cuttings, treatment 2 plots were cut four times, treatment 3 plots nine times, and treatment 4 plots 14 times.

Samples for carbohydrate analyses were collected at the start of the experiment and prior to each 6-week cutting event, a total of nine sampling dates. Unfortunately, the last set of samples (December 1992) was spoiled during a freezer malfunction, so was dropped from the study.

On each sampling date, an increment borer (4.3 mm diameter) was used to extract two 3-cm-long wood cores from both the stumps and large lateral roots of two randomly selected trees in each plot (10 trees per treatment). No tree was sampled more than once. Stem cores were taken 10

cm above the ground, and root cores were taken at a distance of approximately 8 cm from the stem. Immediately after extraction, the bark was removed from the cores, which were then placed in vials in an ice-filled cooler. In the lab, vials were stored in a freezer at 0° C.

For each sampled tree, the stump basal diameter and sampled-root diameters were recorded for use as covariates. Stump basal diameters were measured with a diameter tape, and root diameters with a caliper. Stump basal diameters ranged from 9.5 cm to 33.0 cm, with a mean of 21.0 cm. Diameters of sampled roots were generally between 2.5 cm and 8.0 cm, with a mean of 4.9 cm.

The fresh weight of prunings removed from cored trees was recorded in the field and a subsample (or the complete sample, if small) was returned to the lab. The combined fresh weight of coppice production from all trees in each plot was also recorded. In the lab, subsamples were oven-dried at 65° C until constant weight. Subsample dry weights, as a percentage of original fresh weights, were then used to calculate the weight of dry matter produced by sampled plants and whole plots during the growth interval.

<u>Carbohydrate analysis</u>

Wood cores were freeze-dried as soon as possible after collection, and then were ground to pass through a 40-mesh screen. For each tree, the two stem cores were ground

together, as were the two root cores, forming composite samples for each plant component.

These samples were analyzed using the perchloric acid/anthrone method to measure starch and soluble sugars (McCready et al., 1950; Yemm and Willis, 1954). In this method, four washings of hot ethanol are used to extract soluble sugars from the ground sample. The supernatant is poured into a flask for later sugar determination. The remaining solid residue is washed two times with 52% perchloric acid to solubilize and extract the starch. The solubilized starch solution is reacted with a mixture of anthrone and sulfuric acid to hydrolyze the starch to glucose, and produce a green color. Absorption at 620 nm is determined using a spectrophotometer (Yemm and Willis, 1954), and absorbances are regressed against readings from a set of standard solutions of glucose. A correction factor of 0.9 is used to convert glucose equivalents to starch (McCready et al., 1950). The soluble sugar solution is also reacted with the anthrone/sulfuric acid mixture to determine glucose content.

In a comparison of six methods of starch quantification—three using perchloric acid and three using enzymes to hydrolyze starch—Rose et al. (1991) found that the method used in the present study was superior to the others in terms of technical simplicity, required equipment, and efficiency when processing large numbers of samples.

Statistical analysis

All variables were analyzed using analysis of covariance (SAS Institute, 1988). Variables considered for both roots and stems included soluble sugar, starch, total reserve carbohydrates (the sum of sugar and starch), and sugar percentage. Biomass production during growth intervals was also included.

For gliricidia stems, stump basal diameter was used as a covariate to reduce experimental error that might result from sampling trees of different sizes. For roots, root diameter served the same purpose. For both stems and roots, "elapsed time since last cut" was also used as a covariate. This was necessary because sampling was sometimes unavoidably delayed, resulting in sampling intervals of unequal length.

Analysis of covariance examined data that were organized in three ways: (1) pooled observations to evaluate treatment effects during the entire study period; (2) observations from individual sampling dates to evaluate treatment effects on each date; and (3) observations within individual treatments to evaluate time effects within each treatment. Means were compared using Duncan's multiple range test at the 5% level of significance.

In addition to the above analyses, analysis of variance (ANOVA) was used to evaluate reserve carbohydrate concentrations in roots versus stems. Covariates were not

required for root-versus-stem comparisons because samples from both plant parts were collected from the same trees, at the same times.

The association between dry matter production and reserve carbohydrates in the 6-week and 3-week treatments during the wet season was evaluated using linear regression and correlation analysis. Only wet-season values were included in order to remove the confounding effect of weather. For this analysis, mean dry matter production and mean carbohydrate concentrations were calculated for each of five growth intervals (n=5). Additionally, linear relationships in all three cutting treatments during the last growth interval were analyzed. This analysis used plot means (n=15). All analyses used carbohydrate values from the beginning of a growth interval and biomass values from the end.

Experimental Results

Reserve carbohydrate concentrations

Soluble sugar. Analysis of covariance of all sampling dates combined revealed significant treatment effects for both stem and root sugar (Table 1). The two most frequently cut treatments (3-week, and 6-week) had higher sugar concentrations than the uncut control and the seasonally cut treatment. This trend was most pronounced in the roots, where the two frequently cut treatments had sugar

concentrations more than 20 mg g^{-1} higher than either of the other two treatments.

Significant treatment effects were also found for stem and root sugar when sampling dates were examined individually. For stem sugar, significant differences between treatments were first noted for the fifth sample period—June 16 (Table 2, Figure 2). On that date, the 3-week and 6-week treatments had sugar concentrations significantly higher than the control, a difference which persisted through the end of the experiment. By July 29, stem sugar in the 3-week treatment was also significantly higher than in the seasonally cut treatment. During the last two sample periods (September 10 and October 21), stem sugar concentrations in both the 3-week and 6-week treatments were significantly higher than those in the other two treatments.

Root sugar concentrations on individual sampling dates followed the same pattern as stem sugar concentrations, but treatment effects emerged earlier and differences between treatments were larger (Table 3, Figure 3). Significant differences were first noted for the March 5 sampling period, but these followed no pattern that could be attributed to the applied treatments. At the time these samples were taken, the treatments with the highest and lowest values had received the same number of cuts. The dominant trend for root sugar first became apparent on

Table 1. *Gliricidia sepium*: Mean reserve carbohydrate concentrations for each treatment, all sample dates combined.

A. STEM

Treatment[1]	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	31.0 b	38.9 a	70.0 a
2	30.2 b	26.4 b	56.6 b
3	36.0 a	20.5 c	56.5 b
4	35.4 a	17.8 c	53.2 b

B. ROOT

Treatment	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	32.2 b	158.6 a	190.8 a
2	34.0 b	153.3 a	187.3 ab
3	54.9 a	123.0 b	177.9 ab
4	56.1 a	110.1 b	166.2 b

[1]Treatment 1: uncut control; Treatment 2: cut twice; Treatment 3: cut at 6-week intervals, a total of 7 cuts; Treatment 4: cut at 3-week intervals, a total of 12 cuts.

[2]Each mean is based on 80 trees, ten from each of eight sample dates. Means were compared using Duncan's multiple range test at the 5% level. Means followed by the same letter are not significantly different.

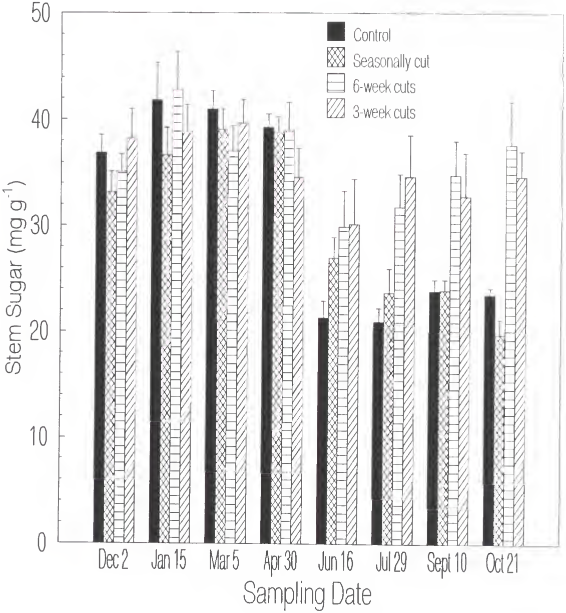

Figure 2. Variations in stem sugar concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

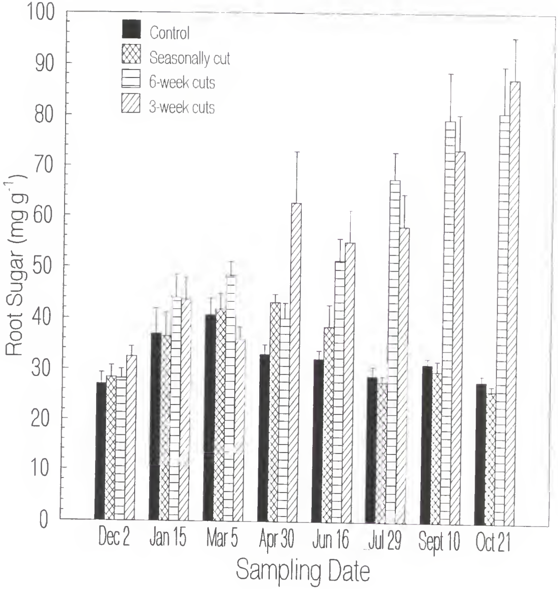

Figure 3. Variations in root sugar concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

Table 2. *Gliricidia sepium*: mean stem carbohydrates in each treatment, on eight sampling dates from December, 1991 to October, 1992.

Sample Date	Sugar[1] ($mg\ g^{-1}$)				Starch ($mg\ g^{-1}$)				Total ($mg\ g^{-1}$)			
	Treatment[2]				Treatment[2]				Treatment[2]			
	1	2	3	4	1	2	3	4	1	2	3	4
2 Dec	36.9 a	33.1 a	35.1 a	38.2 a	42.3 a	46.8 a	42.0 a	46.8 a	79.2 a	79.9 a	77.1 a	85.1 a
15 Jan	41.8 a	36.7 a	42.8 a	38.8 a	47.2 ab	27.2 b	51.8 a	30.6 ab	88.9 a	63.8 b	94.6 a	69.5 b
5 Mar	40.9 a	39.0 a	37.0 a	39.6 a	43.4 ab	56.2 a	37.3 b	38.3 ab	84.3 ab	95.2 a	74.3 b	77.9 ab
30 Apr	39.2 a	38.8 a	39.0 a	34.6 a	37.4 a	14.8 b	12.4 b	11.6 b	76.6 a	53.6 b	51.4 b	46.2 b
16 Jun	21.3 b	27.0 ab	29.9 a	30.1 a	24.4 a	10.2 b	5.3 bc	2.4 c	45.7 a	37.2 ab	35.1 ab	32.5 b
29 Jul	20.9 c	23.7 bc	31.7 ab	34.6 a	25.2 a	12.3 b	4.0 c	3.2 c	46.1 a	36.0 ab	35.7 b	37.8 ab
10 Sep	23.8 b	23.9 b	34.8 a	32.8 a	37.7 a	19.9 b	5.1 c	5.2 c	61.6 a	43.8 b	39.9 b	38.0 b
21 Oct	23.5 b	19.8 b	37.7 a	34.7 a	53.9 a	23.6 b	6.1 c	4.4 c	77.4 a	43.4 b	43.8 b	39.1 b

[1]Each mean is based on ten sample trees. Treatment means for each carbohydrate variable were compared on each sampling date, using Duncan's multiple range test at the 5% level. Means in each sampling group (same date and variable) that are followed by the same letter are not significantly different.

[2]Trt 1 = uncut control; Trt 2 = cut twice; Trt 3 = cut at 6-week intervals; Trt 4 = cut at 3-week intervals.

Table 3. *Gliricidia sepium*: mean root carbohydrates in each treatment, on eight sample dates from December, 1991 to October, 1992.

Sample Date	Sugar[1] ($mg\ g^{-1}$)				Starch ($mg\ g^{-1}$)				Total ($mg\ g^{-1}$)			
	Treatment[2]				Treatment[2]				Treatment[2]			
	1	2	3	4	1	2	3	4	1	2	3	4
2 Dec	27.1 a	28.4 a	28.2 a	32.5 a	202.3 a	181.0 a	187.0 a	190.3 a	229.3 a	209.5 a	215.1 a	222.8 a
15 Jan	37.0 a	36.5 a	44.1 a	43.7 a	221.7 a	181.5 ab	200.1 a	144.5 b	258.7 a	218.0 ab	244.2 a	188.1 b
5 Mar	40.6 ab	41.8 ab	48.3 a	35.8 b	145.3 a	163.2 a	156.6 a	150.8 a	185.9 a	205.0 a	204.9 a	186.6 a
30 Apr	33.0 b	43.2 b	40.0 b	62.7 a	142.9 a	117.1 a	127.0 a	93.2 a	175.9 a	160.3 a	167.1 a	155.9 a
16 Jun	32.2 b	38.4 b	51.3 a	55.0 a	110.9 a	114.1 a	75.4 b	81.9 ab	143.1 a	152.6 a	126.7 a	136.9 a
29 Jul	28.8 b	27.6 b	67.5 a	58.1 a	138.2 a	165.3 a	66.0 b	58.8 b	167.0 ab	192.8 a	133.5 ab	116.9 b
10 Sep	31.2 b	29.8 b	79.3 a	73.4 a	150.2 a	133.7 a	61.4 b	70.2 b	181.4 a	163.5 ab	140.7 b	143.6 ab
21 Oct	27.9 b	26.0 b	80.6 a	87.2 a	157.1 ab	170.6 a	110.4 bc	91.4 c	185.0 a	196.6 a	190.9 a	178.6 a

Each mean is based on ten sample trees. Treatment means for each carbohydrate variable were compared on each sampling date, using Duncan's multiple range test at the 5% level. Means in each sampling group (same date and variable) that are followed by the same letter are not significantly different.

Trt 1 = uncut control; Trt 2 = cut twice; Trt 3 = cut at 6-week intervals; Trt 4 = cut at 3-week intervals.

the April 30 sampling date, when the 3-week treatment was significantly higher than all other treatments. By the next sampling date (June 16), the 6-week treatment was also significantly higher than the control and the seasonally cut treatment. The divergence in root sugar concentrations between the two frequently cut treatments and the other two treatments progressively increased through the succeeding sampling dates (July 29, September 10, October 21). By the last sampling date, the frequently pruned treatments had root sugar concentrations 50 to 60 mg g^{-1} higher than the control and the seasonally cut treatment.

Within-treatment comparisons of changes in stem sugar concentrations over time revealed a distinct contrast between the two frequently pruned treatments and the other treatments (Tables 4-7). In the control and the seasonally cut treatment, stem sugar concentrations decreased significantly between April 30 and June 16, and then remained relatively constant through October 21. This sharp decrease did not occur in the 3-week and 6-week treatments, which maintained fairly consistent stem sugar levels during the course of the experiment. In the two frequently pruned treatments, no sampling date was significantly different from another.

Within-treatment comparisons of changes in root sugar over time revealed different patterns than those observed in stem sugar (Tables 4-7). Root sugar resembled stem sugar in

that concentrations in the control and seasonally cut treatment were generally similar to one another, as were concentrations in the 3-week and 6-week treatments. However, root sugar differed from stem sugar in that the control and the seasonally cut treatment did not experience a marked decrease in root sugar between April 30 and June 16. Root sugar concentrations tended to be higher (sometimes significantly higher) from January through June than from July through December, but the sharp decrease that was observed in stem sugar was absent. An equally pronounced difference between stem sugar and root sugar was observed in the 3-week and 6-week treatments. In these two treatments, root sugar concentrations increased as the harsh pruning regime progressed. Values from the last sampling dates were significantly higher than those from the early sampling dates.

Analysis of variance comparing stem and root sugar in each treatment, all sampling dates combined, illustrated the effect of cutting frequency (Table 8). In the uncut control, there was no significant difference between stem sugar concentration and root sugar concentration. In all three cutting treatments, however, root sugar was significantly higher than stem sugar. The difference increased with the frequency of cutting. In the seasonally cut treatment, root sugar was less than 4 mg g^{-1} higher than

Table 4. *Gliricidia sepium*: Comparisons of carbohydrate means in the control treatment.

STEM:

Date	Sugar[1] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	36.9 a	42.3 ab	79.2 ab	47.1 a
15 Jan 92	41.8 a	47.2 a	88.9 a	48.3 a
5 Mar 92	40.9 a	43.4 ab	84.3 a	51.6 a
30 Apr 92	39.2 a	37.4 ab	76.6 ab	52.2 a
16 Jun 92	21.3 b	24.4 b	45.7 c	48.9 a
29 Jul 92	20.9 b	25.2 b	46.1 c	46.6 a
10 Sep 92	23.8 b	37.7 ab	61.5 bc	39.7 ab
21 Oct 92	23.5 b	53.9 a	77.4 ab	31.3 b

ROOT:

Date	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	27.1 b	202.3 ab	229.3 ab	12.1 b
15 Jan 92	37.0 ab	221.7 a	258.7 a	14.1 ab
5 Mar 92	40.6 a	145.3 abc	185.9 abc	24.4 a
30 Apr 92	33.0 ab	142.9 abc	175.9 bc	20.1 ab
16 Jun 92	32.2 ab	110.9 c	143.1 c	24.4 a
29 Jul 92	28.8 b	138.2 bc	167.0 bc	22.2 ab
10 Sep 92	31.2 ab	150.2 abc	181.4 abc	19.9 ab
21 Oct 92	27.9 b	157.1 abc	185.0 abc	16.2 ab

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 5. *Gliricidia sepium*: Comparisons of carbohydrate means in the seasonally cut treatment.

STEM:

Date	Sugar[1] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	33.1 ab	46.8 a	79.9 ab	44.1 cd
15 Jan 92	36.7 a	27.2 b	63.8 bc	59.0 abc
5 Mar 92	39.0 a	56.2 a	95.2 a	42.6 d
30 Apr 92	38.8 a	14.8 b	53.6 cd	73.1 a
16 Jun 92	27.0 bc	10.2 b	37.2 d	73.2 a
29 Jul 92	23.7 c	12.4 b	36.0 d	65.6 ab
10 Sep 92	23.9 c	19.9 b	43.8 cd	56.1 bcd
21 Oct 92	19.8 c	23.7 b	43.4 cd	47.9 cd

ROOT:

Date	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	28.4 cd	181.0 a	209.5 a	14.5 c
15 Jan 92	36.5 abcd	181.5 a	218.0 a	17.5 bc
5 Mar 92	41.8 ab	163.2 a	205.0 a	21.1 abc
30 Apr 92	43.2 a	117.1 a	160.3 a	31.6 a
16 Jun 92	38.5 abc	114.1 a	152.6 a	28.7 ab
29 Jul 92	27.6 cd	165.3 a	192.9 a	15.6 bc
10 Sep 92	29.8 bcd	133.7 a	163.5 a	21.1 abc
21 Oct 92	26.0 d	170.6 a	196.6 a	17.6 bc

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 6. *Gliricidia sepium*: Comparisons of carbohydrate means in the 6-week treatment.

STEM:

Date	Sugar[1] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	35.1 a	42.0 a	77.1 ab	47.3 b
15 Jan 92	42.8 a	51.8 a	94.6 a	49.5 b
5 Mar 92	37.0 a	37.3 a	74.3 ab	55.2 b
30 Apr 92	39.0 a	12.4 b	51.4 bc	76.9 a
16 Jun 92	29.9 a	5.3 b	35.1 c	85.2 a
29 Jul 92	31.7 a	4.0 b	35.7 c	88.5 a
10 Sep 92	34.8 a	5.1 b	39.9 c	87.6 a
21 Oct 92	37.7 a	6.1 b	43.8 c	85.0 a

ROOT:

Date	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	28.2 c	187.0 ab	215.2 ab	13.6 c
15 Jan 92	44.1 bc	200.1 a	244.2 a	18.5 c
5 Mar 92	48.3 bc	156.6 abc	204.9 abc	24.3 c
30 Apr 92	40.1 c	127.0 bcd	167.1 bcd	27.3 bc
16 Jun 92	51.3 bc	75.4 de	126.7 d	44.7 ab
29 Jul 92	67.5 ab	66.0 de	133.5 d	51.1 a
10 Sep 92	79.3 a	61.4 e	140.7 cd	57.8 a
21 Oct 92	80.6 a	110.4 cde	191.0 abcd	47.0 a

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 7. *Gliricidia sepium*: Comparisons of carbohydrate means in the 3-week treatment.

STEM:

Date	Sugar[1] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	38.2 a	46.8 a	85.1 a	46.9 c
15 Jan 92	38.8 a	30.6 a	69.5 ab	60.4 c
5 Mar 92	39.6 a	38.3 a	77.9 a	54.2 c
30 Apr 92	34.6 a	11.6 b	46.2 bc	75.6 b
16 Jun 92	30.1 a	2.4 b	32.5 c	92.4 a
29 Jul 92	34.6 a	3.2 b	37.8 c	91.1 a
10 Sep 92	32.8 a	5.2 b	38.0 c	87.0 ab
21 Oct 92	34.7 a	4.4 b	39.1 c	88.6 ab

ROOT:

Date	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})	Sugar (%)
2 Dec 91	32.5 d	190.3 a	222.8 a	16.2 c
15 Jan 92	43.7 cd	144.5 abc	188.1 ab	24.6 bc
5 Mar 92	35.8 cd	150.8 ab	186.6 ab	20.8 c
30 Apr 92	62.7 abc	93.2 bcd	155.9 ab	45.3 ab
16 Jun 92	55.0 bcd	81.9 bcd	136.9 b	45.6 ab
29 Jul 92	58.1 bcd	58.8 d	116.9 b	52.1 a
10 Sep 92	73.4 ab	70.2 cd	143.6 ab	55.5 a
21 Oct 92	87.2 a	91.4 bcd	178.6 ab	50.2 a

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 8. *Gliricidia sepium*: Within-treatment comparisons of root and stem carbohydrates.

Treatment[1]	Plant Component	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	Root	32.2 a	158.6 a	190.8 a
	Stem	31.0 a	38.9 b	69.9 b
2	Root	34.0 a	153.3 a	187.3 a
	Stem	30.2 b	26.4 b	56.6 b
3	Root	54.9 a	123.0 a	177.9 a
	Stem	36.0 b	20.5 b	56.5 b
4	Root	56.1 a	110.1 a	166.2 a
	Stem	35.4 b	17.8 b	53.3 b

[1]Treatment 1 = uncut control; Treatment 2 = cut twice; Treatment 3 = cut at 6-week intervals; Treatment 4 = cut at 3-week intervals.

[2]Each mean is based on 80 trees, ten from each of eight sample dates. Means were compared using t-tests of least squares means at the 5% level. Means in each sampling group (same treatment and carbohydrate variable) that are followed by the same letter are not significantly different.

stem sugar; in the 3-week and 6-week treatments it was approximately 20 mg g^{-1} higher than stem sugar.

Starch. As with soluble sugar, analysis of covariance (all sampling dates combined) revealed significant treatment effects for starch (Table 1). Starch concentrations decreased as cutting frequency increased. In both stems and roots, starch concentrations in the two most frequently cut treatments (3-week, and 6-week) were significantly lower than those in the control and the seasonally cut treatment. Stem starch—but not root starch—in the seasonally cut treatment was also significantly different from the control.

Analysis of samples collected on individual sampling dates also revealed significant treatment effects for stem and root starch. For stem starch, the second and third sampling dates (January 16 and March 5) showed significant differences among treatments (Table 2, Figure 4). However, it is believed that these differences resulted not from treatment effects, but rather from the high variability found in starch samples and the presence of several unusually large values that distorted results. Dry-season starch values, in particular, were highly variable, as illustrated by the error bars in Figure 4.

On April 30—the fourth sampling date and first wet-season date—very obvious treatment effects were noted. Stem starch concentration in the control was significantly different from all other treatments, and more than twice as

large as the next highest value. By June 16 in the 3-week treatment, and July 29 in the 6-week treatment, stem starch was also significantly lower than in the seasonally cut treatment. In every case, significant differences, once noted, continued through to the final sampling date—October 21. After differences in stem starch concentration developed, they were very large. In general, stem starch concentration in the seasonally cut treatment was about 50% that of the uncut control, and stem starch in the 3-week and 6-week treatments was approximately 25% that of the seasonally cut treatment.

For root starch, significant treatment effects appeared on June 16, the fifth sampling date (Table 3, Figure 5). On this date, root starch in the 3-week and 6-week treatments was considerably lower than in the two other treatments. This difference was significant for the 6-week treatment. During the next two sampling dates (July 29 and September 10), root starch in the control and seasonally cut treatment increased, and these two treatments were significantly higher than the two frequently cut treatments. Interestingly, by October 21, root starch had begun to increase in the 3-week and 6-week treatments (but concentrations were still lower than in the other treatments). On this date, the 6-week treatment was not significantly different from the control.

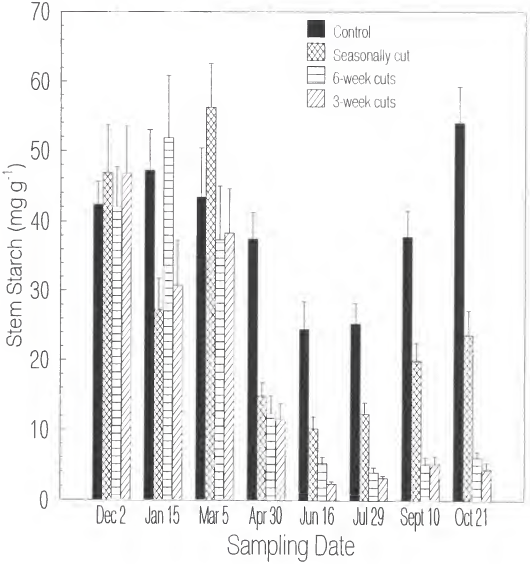

Figure 4. Variations in stem starch concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

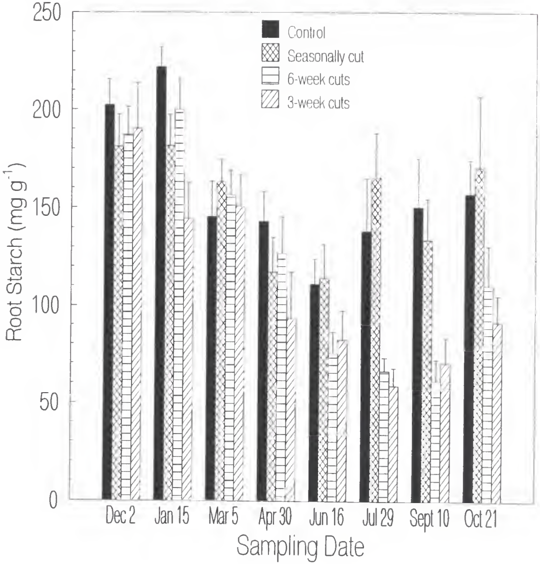

Figure 5. Variations in root starch concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

Within-treatment comparisons of stem starch concentrations over time clearly revealed the effect of cutting (Tables 4-7). By April 30—the first wet-season sampling date—all three cutting treatments experienced marked decreases in stem starch. A decrease was also noted in the control, but it was much less severe than in the cutting treatments.

In the 3-week and 6-week treatments, stem starch on the last five sampling dates was significantly lower than on the first three sampling dates. Stem starch concentrations declined to approximately 5 mg g^{-1}, then stabilized. In the seasonally cut treatment, stem starch on the last five sampling dates was significantly lower than on December 2 and March 5, but not significantly lower than on January 15. In this treatment, stem starch concentrations gradually increased from June 16 to October 21, when no cutting was done.

In the control—which provided baseline data on the effect of season on carbohydrate concentrations—stem starch concentrations were at a low of approximately 25 mg g^{-1} during June and July, and then increased to 40 to 50 mg g^{-1} with the approach of the dry season. Stem starch on October 21 and January 15 was significantly higher than on June 16 and July 29.

Within-treatment comparisons of root starch over time revealed patterns similar to those observed in stem starch,

i.e., starch concentrations decreased with cutting (Tables 4-7). However, the effects were not so clearly defined as in stem starch. In the 3-week and 6-week treatments, root starch on the last five sampling dates tended to be lower than on the first three sampling dates but, in contrast to stem starch, significant differences were not revealed for all comparisons. In the seasonally cut treatment, no date was significantly different from another.

Root starch in the control followed the trend observed for stem starch. Root starch concentrations decreased to a low of approximately 110 mg g^{-1} on June 16, and reached a dry-season high of approximately 220 mg g^{-1} on January 15. Root starch on June 16 and July 29 was significantly lower than on January 15. The data from the June 16 sampling date were also significantly lower than those from December 2.

In all treatments, root starch was significantly higher than stem starch (Table 8). This difference increased with cutting. In the uncut control, root starch was approximately four times higher than stem starch; in the cutting treatments, it was approximately six times higher than stem starch.

Total reserve carbohydrates. Analysis of covariance of all sampling dates combined revealed significant treatment effects for total reserve carbohydrates in both stems and roots (Tables 2 and 3). In stems, the control had a significantly higher concentration of reserve

carbohydrates than the cutting treatments, including the seasonally cut treatment which had a value almost identical to the much more frequently cut 3-week and 6-week treatments. Cutting, however, altered the composition of reserve carbohydrates (as indicated by sugar percent of total reserve carbohydrates) (Table 9). Stem sugar percentage in the control was significantly lower than in the seasonally cut treatment, which had values significantly lower than in the 3-week and 6-week treatments.

In roots, total reserve carbohydrates tended to decrease as cutting frequency increased, but only the control and the 3-week treatment were significantly different. As with stems, the composition of root carbohydrates was altered by cutting. The root sugar percentages in the control and seasonally cut treatment were significantly lower than those in the 3-week and 6-week treatments.

When sampling dates were examined individually, significant treatment effects were revealed for both stem and root reserve carbohydrates (Tables 2 and 3). The most pronounced cutting effect was found in stems (Figure 6). By the April 30 sampling date, total stem carbohydrates in the control were significantly higher than in any of the three cutting treatments. During the next two sampling periods (June 16 and July 29), the difference between the control and the cut treatments decreased. Total stem carbohydrates

in the control were significantly higher than only the 3-week treatment on June 16, and the 6-week treatment on July 29. This diminishment of differences followed a large decrease in stem starch in the control during this period. On the last two sampling dates (September 10 and October 21), stem starch in the control increased and this treatment was again significantly higher than the three cutting treatments. Total reserve carbohydrate concentrations in the three cutting treatments were very similar to one another on the last five sampling dates.

Treatment effects were much less apparent for total root carbohydrates (Table 3, Figure 7). Significant effects were revealed only on the July 29 and September 10 sampling dates. The control was significantly higher than the 3-week treatment on July 29, and the 6-week treatment on September 10. On the last sampling date (October 21), total root carbohydrate concentrations were very similar in all treatments. The increase in root starch observed in the 3-week and 6-week treatments on that date contributed to this outcome.

Within-treatment comparisons of total reserve carbohydrates in both stems and roots revealed significant time effects (Tables 4-7). In the three cutting treatments, total stem carbohydrate concentrations during the second half of the study were generally significantly lower than

Table 9. *Gliricidia sepium*: The effect of pruning frequency on the composition of reserve carbohydrates.

Treatment[1]	Stem Sugar[2] (%)	Root Sugar (%)
1	45.7 c	19.2 b
2	57.7 b	21.0 b
3	71.9 a	35.5 a
4	74.5 a	38.8 a

[1]Treatment 1: uncut control; Treatment 2: cut twice; Treatment 3: cut at 6-week intervals, a total of 7 cuts; Treatment 4: cut at 3-week intervals, a total of 12 cuts.

[2] Expressed as a percentage of total reserve carbohydrates. Each mean is based on 80 trees, ten from each of eight sample dates (n=80). Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different.

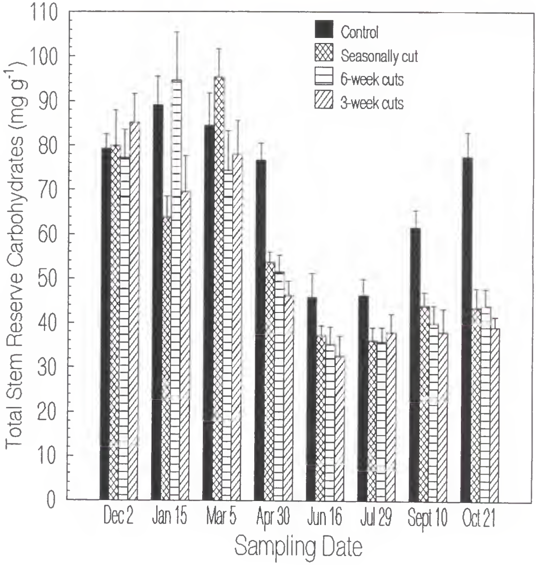

Figure 6. Variations in total stem carbohydrate concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

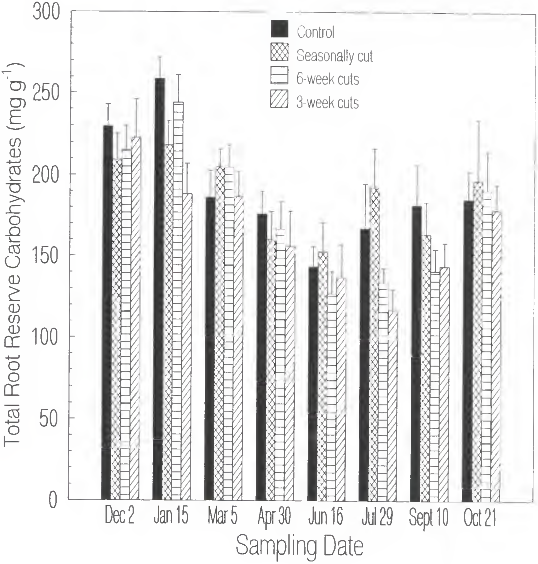

Figure 7. Variations in total root carbohydrate concentrations in *Gliricidia sepium*, December 1991 to October 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

those recorded during the first half of the study. In the 3-week and 6-week treatments, lower total stem carbohydrate values resulted from reduced starch levels; sugar levels varied little. In the seasonally cut treatment, decreases in both sugar and starch contributed to lower total stem carbohydrate values.

All treatments had their lowest total stem carbohydrate concentrations during June and July, but frequent cutting reduced the magnitude of differences between dates. The "growing-season slump" was most obvious in the control, which recorded its lowest values for both stem sugar and stem starch during this period. In the control, total stem carbohydrates on the June 16 and July 29 sampling dates were almost 50% lower (a significant difference) than on the January 15 and March 5 sampling dates. Other than the June/July decrease, total stem carbohydrate levels varied little in the control during the experiment. On the five sampling dates from October 21 through April 30, values were not significantly different and ranged from approximately 77 mg g^{-1} to 89 mg g^{-1}. The September 10 value of 62 mg g^{-1} was significantly different only from the January and March sampling dates.

Because root starch concentrations in the control and seasonally cut treatment were always substantially larger than sugar concentrations, within-treatment comparisons of total root carbohydrates in these two treatments revealed

trends almost identical to those observed for root starch. In the seasonally cut treatment, no date was significantly different from another. In the control, total root carbohydrate concentrations followed the general trend observed in stems. Concentrations were lowest on June 16 and highest on January 15. The values on April 30, June 16, and July 29 were significantly lower than that of January 15. The June 16 sampling date was also significantly lower than December 2.

In the 3-week and 6-week treatments, root sugar increased and root starch (except on October 21) generally decreased as the study progressed. By the second half of the study, sugar and starch contributed almost equally to total root carbohydrates. In general, cutting in these two treatments decreased total root carbohydrates from April 30 through September 10 (the fourth through seventh sampling dates). On October 21, increases in root starch contributed to increases in total root carbohydrates.

As noted above, comparisons of total stem carbohydrates within the 3-week and 6-week treatments revealed sharp differences between samples collected during the first half of the study and those from the second half. Distinctions were not as clear-cut for total root carbohydrates. In the 6-week treatment, June 16 and July 29 were significantly lower than December 2, January 15, and March 5; September 10 was significantly lower than December 2 and January 15; and

April 30 was significantly lower than January 15. In the 3-week treatment, June 16 and July 29 were significantly lower than December 2. In neither of the frequently cut treatments were total root carbohydrates on the last sampling date (October 21) significantly different from those on any other date.

In all treatments, due to high concentrations of root starch, the roots had significantly more total reserve carbohydrates than stems (Table 8). This disparity was apparently increased by the cutting treatments. In the uncut control, total reserve carbohydrates in roots were approximately 2.7 times higher than in stems; in the cutting treatments, root values were 3.1 to 3.3 times higher than stem values.

Dry matter production

Treatment effects. Cumulative dry matter production during one year—December 9, 1991 to December 4, 1992—was 1060 g $tree^{-1}$ in the seasonally cut treatment (3 cuts), 171 g $tree^{-1}$ in the 6-week treatment (8 cuts), and 77 g $tree^{-1}$ in the 3-week treatment (13 cuts). All treatment means were significantly different from one another (Table 10).

Significant differences in cumulative biomass production among treatments were also noted during the dry and wet seasons (Table 10). During the long dry season (December 9, 1991 to March 10, 1992), biomass production in the seasonally cut treatment (1 cut) was significantly

higher than in the 6-week and 3-week treatments, which were cut twice. The seasonally cut treatment produced 31 g tree^{-1}, the 6-week and 3-week treatments produced 17 g tree^{-1}.

The same trend—less dry matter production in the more frequently cut treatments—was observed during the wet season (March 10, 1992 to October 24, 1992, including the short dry period of August). During that period, the seasonally cut treatment (1 cut) produced 999 g tree^{-1}, the 6-week treatment (5 wet-season cuts) produced 143 g tree^{-1}, and the 3-week treatment (10 wet-season cuts) produced 46 g tree^{-1}. All differences were significant.

Only the 3-week and 6-week treatments were cut at regular intervals during the entire study period. Therefore, only these two treatments were compared for dry matter production during individual growth intervals (Table 11). On the January 18 and March 10 sampling dates, when these two treatments had received the same number of cuts, their dry matter production was not significantly different. However, when the 3-week cutting regime was initiated in the 3-week treatment, this treatment produced significantly less biomass (cumulative production from two 3-week growth intervals) than the 6-week treatment. Interestingly, during the final growth interval (December 4 sampling date), when both of these treatments were cut once, the 3-week treatment—which had been subjected to the harshest cutting

regime—produced significantly more biomass than the 6-week treatment.

Within-treatment comparisons of dry matter production during individual growth intervals, in the 3-week and 6-week treatments, revealed significant differences among sampling dates (Tables 12 and 13). For both treatments, the lowest dry matter production (for a growth interval with six weeks of uninterrupted growth) occurred during the first growth interval (January 18 sampling date). For the 6-week treatment, this value (4.8 g tree^{-1}) was significantly lower than the means for all seven subsequent growth intervals. For the 3-week treatment, dry matter production during the first growth interval (4.4 g tree^{-1}) was only slightly higher than, and not significantly different from, values recorded during the fifth, sixth, and seventh growth intervals, when biomass was calculated as the aggregate of two cuts.

In both frequently cut treatments, the greatest dry matter production occurred during the first wet-season growing interval (May 1 sampling date). In the 6-week treatment, production rose from 13 g tree^{-1} on March 10 to 70 g tree^{-1} on May 1. In the 3-week treatment, production doubled from 13 g tree^{-1} on March 10 (1 cut) to 25 g tree^{-1} on May 1 (aggregate of 2 cuts). In both treatments, dry matter production from the May 1 sampling date was significantly higher than that recorded during any other growth interval.

Table 10. *Gliricidia sepium*: Seasonal and cumulative dry matter production in the cutting treatments.

Sample Period	Trt	Number of cuts[1]	Mean production[2] ($g\ tree^{-1}$)	Mean daily productivity ($g\ tree^{-1}\ day^{-1}$)
Dry Season:	2	1	30.8 a	0.33
9 Dec 91 to	3	2	17.4 b	0.19
10 Mar 92	4	2	17.1 b	0.18
Wet Season:	2	2	999.2 a	4.40
10 Mar 92 to	3	7	143.2 b	0.63
24 Oct 92	4	12	46.3 c	0.20
24 Oct 92	2	3	30.0 a	0.73
to	3	8	10.3 c	0.25
4 Dec 92	4	13	14.0 b	0.34
Total:	2	3	1060.0 a	2.93
9 Dec 91 to	3	8	170.9 b	0.47
4 Dec 92	4	13	77.4 c	0.21

[1]Number of cuts refers to the total number of times trees were pruned prior to, but not including, the end date of a sample period.

[2]Means were compared using Duncan's multiple range test at the 5% level. Means for each sample period are not significantly different when followed by the same letter.

Table 11. *Gliricidia sepium*: Comparisons of dry matter production in the 3-week and 6-week treatments, from 9 December 1991 to 4 December 1992.

Harvest Date	Trt[1]	Number of cuts to date	Mean production[2] (g $tree^{-1}$)	Mean daily productivity (g $tree^{-1}$ day^{-1})
18 Jan	3	1	4.8 a	0.12
	4	1	4.4 a	0.11
10 Mar	3	2	12.6 a	0.24
	4	2	12.7 a	0.24
1 May	3	3	70.4 a	1.33
	4	4	25.2 b	0.48
18 Jun	3	4	35.2 a	0.77
	4	6	10.5 b	0.23
31 Jul	3	5	13.6 a	0.32
	4	8	3.8 b	0.09
12 Sept	3	6	11.2 a	0.26
	4	10	3.4 b	0.08
24 Oct	3	7	12.9 a	0.31
	4	12	3.4 b	0.08
4 Dec	3	8	10.3 b	0.25
	4	13	14.0 a	0.34

[1]Treatment 3 = 6-week treatment; Treatment 4 = 3-week treatment.

[2]Means were compared using t-tests of least square means ($P \leq 0.05$). Means at each date are significantly different when followed by different letters. All means are based on 170 trees, 34 from each plot. Treatment 4 dry matter production is the sum of two cuts, except during the 18 January, 10 March, and 4 December sample periods in which only one cut was made.

Table 12. *Gliricidia sepium*: Dry matter production in the 6-week treatment, from 9 December 1991 to 4 December 1992.

Harvest date	Mean production[1] (g $tree^{-1}$)	Mean daily productivity (g $tree^{-1}$ day^{-1})
18 Jan	4.8 d	0.12 d
10 Mar	12.6 c	0.24 c
1 May	70.4 a	1.33 a
18 Jun	35.2 b	0.77 b
31 Jul	13.6 c	0.32 c
12 Sep	11.2 c	0.26 c
24 Oct	12.9 c	0.31 c
4 Dec	10.3 c	0.25 c

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 5 plots, with 34 trees per plot.

Table 13. *Gliricidia sepium*: Dry matter production in the 3-week treatment, from 9 December 1991 to 4 December 1992.

Harvest date	Mean production[1] (g tree^{-1})	Mean daily productivity (g tree^{-1} day^{-1})
18 Jan[2]	4.4 d	0.11 d
10 Mar[2]	12.7 bc	0.24 c
1 May	25.2 a	0.48 a
18 Jun	10.5 c	0.23 c
31 Jul	3.8 d	0.09 d
12 Sep	3.4 d	0.08 d
24 Oct	3.4 d	0.08 d
4 Dec[2]	14.0 b	0.34 b

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Unless otherwise noted, dry matter is the production from two cuts during the sample period. Means are based on 5 plots, with 34 trees per plot.

[2]Dry matter is the production from one cut.

From the May 1 peak, dry matter production steadily decreased in both treatments until the July 31 sampling date, after which production tended to level off. In the 6-week treatment, dry matter production on the four sampling dates from July 31 through December 4 ranged from 14 g $tree^{-1}$ to 10 g $tree^{-1}$. Means were not significantly different. In the 3-week treatment, dry matter production (aggregate of two cuts) on the three sampling dates from July 31 through October 24 ranged from 4 g $tree^{-1}$ to 3 g $tree^{-1}$. Again, there were no significant differences.

For samples collected on October 24, biomass was sorted into leaves and stems, and the mean dry weight of each component was calculated separately. Additionally, ten trees were harvested in the control treatment for comparison with other treatments. On the sampling date, the control trees had not been cut for approximately 23 months, and trees in the seasonally cut treatment had not been cut for approximately 32 weeks. Trees in the 6-week treatment had six weeks of growth; those in the 3-week treatment had three weeks of growth. Mean dry matter production during these growth periods (n=10 trees) was 1549 g $tree^{-1}$ in the control, 976 g $tree^{-1}$ in the seasonally cut treatment, 13 g $tree^{-1}$ in the 6-week treatment, and 1.4 g $tree^{-1}$ in the 3-week treatment. The proportion of total dry matter that was composed of leaves varied considerably among treatments. In the control, leaf dry matter accounted for 9.0 % of total

aboveground biomass, in the seasonally cut treatment 19.9 %, in the 6-week treatment 61.3 %, and in the 3-week treatment 69.4 %. Each leaf percentage mean was different from the others at the 5% level of significance.

Dry matter production as function of carbohydrate concentrations. The association between dry matter production and reserve carbohydrate levels was evaluated in the 6-week and 3-week treatments during the wet season, using linear regression and correlation analysis. The analysis used means for each of five growth intervals (n=5), which ended on the April 30, June 16, July 29, September 10, and October 21 sampling dates. Each biomass mean was based on the production of 170 trees (34 trees per plot), and each carbohydrate mean was based on ten trees (2 trees per plot). Analyses used carbohydrate values from the beginning of a growth interval and biomass values from the end.

Correlation analysis revealed a significant linear association between dry matter production and many of the reserve carbohydrate variables (Table 14). In the 6-week treatment, significant correlations ($P \leq 0.05$) were found between dry matter and stem starch, total stem carbohydrates, stem sugar percentage, root starch, and total root carbohydrates. In the 3-week treatment, significant correlations ($P \leq 0.05$) were found between dry matter and stem starch, total stem carbohydrates, stem sugar percentage, and root starch. Also in the 3-week treatment,

correlations between dry matter and stem sugar, total root carbohydrates, and root sugar percentage were significant at the 10% level of significance. Figure 8 presents regressions of dry matter against stem starch in the 3-week and 6-week treatments.

All three cutting treatments were harvested on October 24, 1992 and then were allowed to grow undisturbed until December 4, 1992, when they were cut again (Table 10). This was the only time during the study when all three of these treatments were harvested after six weeks of growth. It was, therefore, the only period for which all three cutting treatments could be included in correlation analysis of dry matter and reserve carbohydrates, without the complicating influence of growth intervals of differing duration. Significant linear correlations were found between plot means for dry matter (34 trees per plot) and reserve carbohydrates (2 trees per plot)(Table 15). Results of this analysis were similar to results listed in Table 14 for the 3-week and 6-week treatments during the wet season. The main difference was that, for December biomass, correlation coefficients were very low for both stem and root total reserve carbohydrates. This reflects the similar values recorded for these variables in all treatments on the October sampling date.

Table 14. *Gliricidia sepium*: Correlation coefficients for dry matter as a linear function of reserve carbohydrate concentrations in the 3-week and 6-week treatments.

Y variable	X variable	Correlation Coefficient[1] (r)	
		Treatment[2] 3	Treatment[2] 4
Dry Matter ($g\ tree^{-1}$)	Stem Sugar	0.66 ns	0.93 *
	Stem Starch	0.99 **	0.99 **
	Stem Total	0.99 ***	0.99 **
	Stem Sugar %	-0.99 ***	-0.98 **
	Root Sugar	-0.58 ns	-0.77 ns
	Root Starch	0.96 **	0.98 **
	Root Total	0.98 **	0.96 *
	Root Sugar %	-0.86 ns	-0.96 *

[1]Each correlation is based on means from five sample dates between April 1992 and October 1992 (n=5); only wet-season dates were included. When seemingly identical correlation coefficients show different levels of significance, it is due to rounding of values. Reserve carbohydrate concentrations ($mg\ g^{-1}$) were measured at the beginning of each growth interval. Dry matter was measured at the end of each growth interval.

[2]Treatment 3 = 6-week cutting interval; Treatment 4 = 3-week cutting interval.

Table 15. *Gliricidia sepium*: Correlation coefficients for dry matter as a linear function of reserve carbohydrate concentrations for the period from 24 October 1992 to 4 December 1992.

Y variable	X variable	Correlation Coefficient[1] (r)
Dry Matter (g $tree^{-1}$)	Stem Sugar	-0.83 ***
	Stem Starch	0.88 ***
	Stem Total	0.11 ns
	Stem Sugar %	-0.90 ***
	Root Sugar	-0.84 ***
	Root Starch	0.65 **
	Root Total	0.19 ns
	Root Sugar %	-0.81 ***

[1]Each correlation is based on fifteen plot means, five from each cutting treatment (n=15). Reserve carbohydrate concentrations (mg g^{-1}) were measured at the beginning of the growth interval. Dry matter was measured at the end of the growth interval.

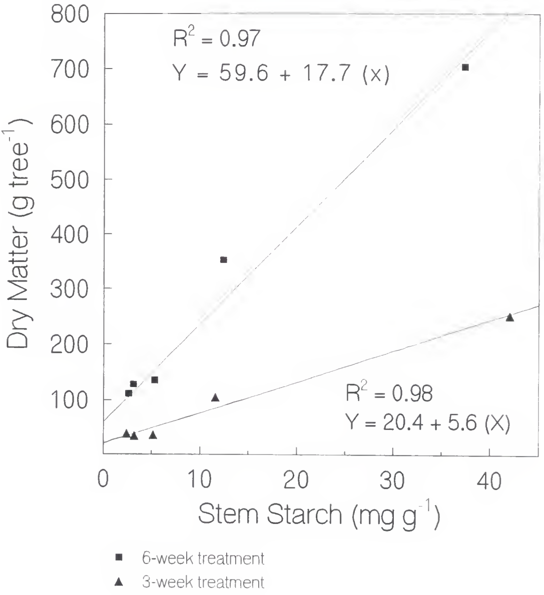

Figure 8. Regression of dry matter on stem starch in the 3-week and 6-week treatments. Each point is based on means for a wet-season sampling date from April to October, 1992.

Effects of Cutting Frequency on Reserve Carbohydrates and Biomass Production in *Leucaena Leucocephala* (Lam.) de Wit

Materials and Methods

Study site

The study was conducted at the main research station of IITA in Ibadan, Nigeria. The site description and weather information are provided at the beginning of the gliricidia section (p. 26). Field work for the leucaena study was conducted from mid-January 1992 through December 1992.

The soil of the experimental plot (WB I, watershed 5) was classified as an Oxic Paleustalf, and texturally as a sandy clay loam. Hedgerows on the site were first established in April 1983 when pre-scarified seeds of leucaena (var. K—26) were sown at a within-row spacing of 25 cm and a between-row spacing of 4.5 m. Starting in August 1983 and continuing through 1988, hedges were cut on average three times per year at 50 cm above the soil surface. All prunings were distributed in the alleys between hedgerows.

For twelve consecutive growing seasons (1983-1988), alleys were cropped using a maize/cowpea (*Vigna unguiculata*) rotation. Maize was sown in the first growing season of each year, and cowpea in the second season. Maize received fertilizer at the rate of 120 kg N ha^{-1} as urea, 26 kg P ha^{-1} as single superphosphate, and 30 kg K ha^{-1} as muriate of potash. After cropping ended in 1988, trees on the site

were cut to ground level several times per year with a tractor-operated mower. All prunings were automatically distributed in the alleys. This treatment was discontinued at the end of 1990, and the site was left undisturbed until initiation of the present study in January, 1992.

When the cutting frequency study began, most trees were between 5 m and 6 m in height, and there was almost complete canopy closure over the alleys. Because of ground-level cutting in 1989 and 1990, each tree had developed as a cluster of stems sprouting from a single woody base. After cutting, new sprouts grew mainly at the perimeters of the woody bases, causing the bases to progressively increase in area after each cycle of cutting and resprouting. Trees included in the study had woody bases with areas ranging from 189 cm^2 to 4657 cm^2, with a mean of 1401 cm^2. The number of stems (with a basal diameter greater than 1 cm) in each clump ranged from 2 to 12, with a mean of 5.1. Stem diameters ranged from 1.0 cm to 6.7 cm, with a mean of 3.2 cm. In total, the study included 464 m of hedgerows and encompassed an area of approximately 0.26 hectares.

At the beginning of the study, the alleys between hedgerows were densely overgrown with *Chromolaena odorata* shrubs which were over 2 m in height. Alleys were manually cleared with cutlasses (machetes), and were kept clear in this manner for the duration of the study.

Experimental design and sampling procedure

The study was set up as a randomized complete block with 5 blocks, 4 treatments, and 18 trees per plot, except in the 3-week treatment which contained 34 trees per plot. More trees were included in the 3-week treatment because it was sampled twice as often as the other treatments, and each tree was to be sampled only once. Buffer areas were located between treatments containing tall plants and those containing more frequently pruned plants in order to minimize the effect of shading. As in the gliricidia study, treatments consisted of:

(1) uncut control;

(2) seasonal cutting—cut at end of long dry season (March), and end of rainy season (October);

(3) cutting at 6-week intervals;

(4) cutting at 6-week intervals during the dry season (January to March), and then at 3-week intervals.

Trees in treatments 2, 3, and 4 were initially cut during the period of January 23 to 24, 1992. At that time, a chainsaw was used to cut all trees to within 25 cm of the ground. During subsequent cuttings, all coppice sprouts were cut to within 1 cm of the stump. Including the initial and final (December 1992) cuttings, treatment 2 plots were cut four times, treatment 3 plots eight times, and treatment 4 plots 13 times.

Samples for carbohydrate analyses were collected at the start of the experiment and prior to each 6-week cutting event, a total of eight sampling dates. Unfortunately, the last set of samples (December 1992) was spoiled during a freezer malfunction, so was dropped from the study.

Collection of wood samples was done somewhat differently for leucaena than for gliricidia due to differences in the size and structure of plant material. Stem diameters were relatively small in the leucaena study, so rather than using an increment borer to extract samples, a saw was used to remove wood disks from two stems per tree, at 10 cm above the root crown. As in the gliricidia study, an increment borer was used to extract two 3-cm-long wood cores from roots. However, because large lateral roots were rare at a depth of less than 20 cm, samples were taken from root crowns.

For each sampled tree, woody-base diameter, and diameter of each sampled stem (measured immediately above the basal swelling) were recorded for use as covariates. Stem diameters were measured with a caliper. A meter stick was used to take two measurements, at right angles to one another, of woody-base diameters. These were averaged to obtain a mean base diameter for each tree, which was later used to calculate clump-base area. Except as noted, sampling procedures were identical to those described for gliricidia.

Carbohydrate analysis

Chemical analysis of ground wood samples followed the procedure described for gliricidia.

Statistical analysis

Statistical analysis followed the procedures described for gliricidia. Only the covariates differed. For leucaena, both stem and root analyses included clump-base area and elapsed time as covariates. Stems used the additional covariate of sampled-stem basal diameter. Possible variability in carbohydrate concentrations, caused by reproductive growth in the control and seasonally cut treatments, was not accounted for in the statistical analyses. The presence of reproductive growth might decrease levels of reserve carbohydrates (Loescher et al., 1990; Kozlowski, 1992).

Experimental Results

Reserve carbohydrate concentrations

Soluble sugar. In contrast to gliricidia, analysis of covariance of all sampling dates combined revealed no significant treatment effects in leucaena for either stem sugar or root sugar (Table 16). Sugar in roots seemed to increase with increased cutting frequency, while sugar in stems decreased, but treatments were not significantly different.

Significant treatment effects, however, were found for both stem and root sugar when sampling dates were examined

individually (Tables 17 and 18, Figures 9 and 10). Stem sugar concentrations in the control tended to be higher than those in the 3-week and 6-week treatments on the last five sampling dates (May 4 through October 27), but significant differences were not always noted. Significant treatment effects were first revealed on the fourth sampling date (June 19), when stem sugar concentrations in the control were significantly higher than those in the other treatments. On August 3, the control was significantly higher than the seasonally cut treatment and the 3-week treatment, but not the 6-week treatment. On the last two sampling dates, the seasonally cut treatment had slightly more stem sugar than the control, and was the only treatment that was significantly different from the others. The seasonally cut treatment was significantly higher than the 3-week treatment on September 15, and significantly higher than both the 3-week and 6-week treatments on October 27. There were no large treatment differences for root sugar concentrations on individual sampling dates.

Within-treatment comparisons of both stem- and root sugar, over time, revealed a distinct contrast between dry-season concentrations and wet-season concentrations (Tables 19-22, Figures 9 and 10). In all treatments, and in both stems and roots, sugar concentrations on January 22 and March 11 were significantly higher than concentrations on

Table 16. *Leucaena leucocephala*: Mean reserve carbohydrate concentrations for each treatment, all sample dates combined.

A. STEM

Treatment[1]	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	27.8 a	18.0 a	45.8 a
2	25.6 a	9.1 b	34.8 b
3	23.6 a	5.6 b	29.2 b
4	23.3 a	6.7 b	30.0 b

B. ROOT

Treatment	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	31.7 a	28.1 a	59.9 a
2	32.5 a	17.7 b	50.2 b
3	34.8 a	11.8 c	46.6 b
4	35.3 a	9.7 c	45.0 b

[1]Treatment 1: uncut control; Treatment 2: cut twice; Treatment 3: cut at 6-week intervals, a total of 6 cuts; Treatment 4: cut at 3-week intervals, a total of 11 cuts.

[2]Each mean is based on 70 trees, ten from each of seven sample dates. Means were compared using Duncan's multiple range test at the 5% level. Means in the same column followed by the same letter are not significantly different.

Table 17. *Leucaena leucocephala*: mean stem carbohydrate concentrations[1] in each treatment, on seven sampling dates from January 1992 to October 1992.

Sample Date	Sugar ($mg\ g^{-1}$)				Starch ($mg\ g^{-1}$)				Total ($mg\ g^{-1}$)			
	Treatment[2]				Treatment				Treatment			
	1	2	3	4	1	2	3	4	1	2	3	4
21 Jan	42.3 a	40.1 a	48.8 a	50.3 a	18.6 a	12.1 a	16.3 a	22.9 a	60.8 ab	52.2 b	65.1 ab	73.2 a
11 Mar	44.8 a	48.0 a	35.3 a	44.6 a	31.4 a	10.7 b	9.3 b	13.1 b	76.2 a	58.6 ab	44.5 b	57.7 b
4 May	23.3 a	17.7 a	18.0 a	20.6 a	25.7 a	4.2 b	3.5 b	3.8 b	49.1 a	21.9 b	21.5 b	24.4 b
19 Jun	19.7 a	14.4 b	13.6 b	11.1 b	12.5 a	6.6 b	2.1 c	1.5 c	32.2 a	21.0 b	15.7 c	12.6 c
3 Aug	22.5 a	14.4 b	17.0 ab	10.4 b	19.1 a	9.3 b	3.2 c	2.9 c	41.6 a	23.6 b	20.2 bc	13.2 c
15 Sep	21.7 a	23.2 a	19.4 ab	14.4 b	11.4 a	4.8 b	2.1 b	2.1 b	33.2 a	28.0 ab	21.5 bc	16.6 c
27 Oct	18.8 ab	20.6 a	14.1 b	12.9 b	7.7 ab	15.6 a	2.2 b	1.4 b	26.6 ab	36.1 a	16.3 bc	14.3 c

[1]Each mean is based on ten sample trees. Treatment means for each carbohydrate variable were compared on each sampling date, using Duncan's multiple range test at the 5% level. Means in each sampling group (same date and variable) that are followed by the same letter are not significantly different.

[2]Trt 1 = uncut control; Trt 2 = cut twice; Trt 3 = cut at 6-week intervals; Trt 4 = cut at 3-week intervals.

Table 18. *Leucaena leucocephala*: mean root carbohydrate concentrations[1] in each treatment, on seven sampling dates, from January 1992 to October 1992.

Sample Date	Sugar ($mg\ g^{-1}$)				Starch ($mg\ g^{-1}$)				Total ($mg\ g^{-1}$)			
	Treatment[2]				Treatment				Treatment			
	1	2	3	4	1	2	3	4	1	2	3	4
21 Jan	51.6 a	51.1 a	55.3 a	56.3 a	29.4 a	26.0 a	23.0 a	17.0 a	81.0 a	77.0 a	78.2 a	73.2 a
11 Mar	46.8 a	55.4 a	51.2 a	59.5 a	35.5 a	26.4 a	15.1 a	25.0 a	82.3 a	81.8 a	66.3 a	84.5 a
4 May	20.9 a	21.8 a	20.2 a	22.8 a	34.5 a	11.0 b	16.1 b	11.5 b	55.4 a	32.8 b	36.3 b	34.4 b
19 Jun	28.7 a	27.3 a	29.4 a	26.4 a	26.8 a	13.5 b	10.8 bc	4.1 c	55.6 a	40.9 b	40.3 b	30.5 b
3 Aug	25.7 a	25.9 a	29.0 a	28.6 a	28.8 a	24.4 a	6.5 b	4.4 b	54.5 a	50.3 a	35.4 b	33.0 b
15 Sep	24.9 a	28.1 a	32.0 a	31.6 a	22.9 a	11.3 b	6.3 bc	3.3 c	47.7 a	39.4 ab	38.3 ab	34.9 b
27 Oct	23.3 ab	18.2 b	26.2 a	22.6 ab	19.5 a	12.5 a	3.8 b	2.1 b	42.8 a	30.7 b	30.0 b	24.8 b

[1]Each mean is based on ten sample trees. Treatment means for each carbohydrate variable were compared on each sampling date, using Duncan's multiple range test at the 5% level. Means in each sampling group (same date and variable) that are followed by the same letter are not significantly different.

[2]Trt 1 = uncut control; Trt 2 = cut twice; Trt 3 = cut at 6-week intervals; Trt 4 = cut at 3-week intervals.

Table 19. *Leucaena leucocephala*: Comparisons of carbohydrate means in the control treatment.

STEM:

Date	Sugar[1] (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	42.3 a	18.6 abc	60.8 ab	69.1 a
11 Mar 92	44.8 a	31.4 a	76.2 a	62.1 ab
4 May 92	23.3 b	25.7 ab	49.1 bc	48.9 b
19 Jun 92	19.7 b	12.5 bc	32.2 cd	62.4 ab
3 Aug 92	22.5 b	19.1 abc	41.6 bcd	55.7 ab
15 Sep 92	21.7 b	11.4 bc	33.2 cd	67.1 ab
27 Oct 92	18.8 b	7.7 c	26.6 d	71.8 a

ROOT:

Date	Sugar (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	51.6 a	29.4 a	81.0 a	65.6 a
11 Mar 92	46.8 a	35.5 a	82.3 a	58.0 ab
4 May 92	20.9 b	34.5 a	55.4 b	38.4 c
19 Jun 92	28.7 b	26.8 a	55.6 b	52.7 abc
3 Aug 92	25.7 b	28.8 a	54.5 b	48.4 bc
15 Sep 92	24.9 b	22.9 a	47.7 b	53.8 abc
27 Oct 92	23.3 b	19.5 a	42.8 b	57.1 ab

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 20. *Leucaena leucocephala*: Comparisons of carbohydrate means in the seasonally cut treatment.

STEM:

Date	Sugar[1] (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	40.1 a	12.1 ab	52.2 ab	77.2 abc
11 Mar 92	48.0 a	10.7 ab	58.6 a	82.3 ab
4 May 92	17.7 b	4.2 b	21.9 c	81.2 abc
19 Jun 92	14.4 b	6.6 ab	21.0 c	69.5 abc
3 Aug 92	14.4 b	9.3 ab	23.6 c	63.6 bc
15 Sep 92	23.2 b	4.8 ab	28.0 c	82.8 a
27 Oct 92	20.6 b	15.6 a	36.1 bc	63.5 c

ROOT:

Date	Sugar (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	51.1 a	26.0 a	77.0 a	68.5 ab
11 Mar 92	55.4 a	26.4 a	81.8 a	70.3 ab
4 May 92	21.8 b	11.0 a	32.8 b	65.4 ab
19 Jun 92	27.3 b	13.5 a	40.9 b	67.7 ab
3 Aug 92	25.9 b	24.4 a	50.3 b	53.4 b
15 Sep 92	28.1 b	11.3 a	39.4 b	70.6 a
27 Oct 92	18.2 b	12.5 a	30.7 b	60.9 ab

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 21. *Leucaena leucocephala*: Comparisons of carbohydrate means in the 6-week treatment.

STEM:

Date	Sugar[1] (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	48.8 a	16.3 a	65.1 a	74.7 c
11 Mar 92	35.3 b	9.3 b	44.5 b	79.0 bc
4 May 92	18.0 c	3.5 c	21.5 c	83.3 ab
19 Jun 92	13.6 c	2.1 c	15.7 c	86.9 ab
3 Aug 92	17.0 c	3.2 c	20.2 c	83.6 ab
15 Sep 92	19.4 c	2.1 c	21.5 c	88.7 a
27 Oct 92	14.1 c	2.2 c	16.3 c	85.5 ab

ROOT:

Date	Sugar (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	55.3 a	23.0 a	78.2 a	71.3 c
11 Mar 92	51.2 a	15.1 abc	66.3 a	78.3 abc
4 May 92	20.2 c	16.1 ab	36.3 b	58.5 d
19 Jun 92	29.4 bc	10.8 bcd	40.3 b	75.1 bc
3 Aug 92	29.0 bc	6.5 bcd	35.4 b	81.5 abc
15 Sep 92	32.0 b	6.3 cd	38.3 b	84.8 ab
27 Oct 92	26.2 bc	3.8 d	30.0 b	88.3 a

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

Table 22. *Leucaena leucocephala*: Comparisons of carbohydrate means in the 3-week treatment.

STEM:

Date	Sugar[1] (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	50.3 a	22.9 a	73.2 a	71.1 c
11 Mar 92	44.6 a	13.1 b	57.7 b	77.5 bc
4 May 92	20.6 b	3.8 c	24.4 c	83.8 ab
19 Jun 92	11.1 bc	1.5 c	12.6 c	88.0 ab
3 Aug 92	10.4 c	2.9 c	13.2 c	77.8 ab
15 Sep 92	14.4 bc	2.1 c	16.6 c	86.6 ab
27 Oct 92	12.9 bc	1.4 c	14.3 c	90.1 a

ROOT:

Date	Sugar (mg g-1)	Starch (mg g-1)	Total (mg g-1)	Sugar (%)
22 Jan 92	56.3 a	17.0 ab	73.2 a	76.4 bc
11 Mar 92	59.5 a	25.0 a	84.5 a	71.8 c
4 May 92	22.8 b	11.5 bc	34.4 b	68.9 c
19 Jun 92	26.4 b	4.1 c	30.5 b	86.6 ab
3 Aug 92	28.6 b	4.4 c	33.0 b	87.1 ab
15 Sep 92	31.6 b	3.3 c	34.9 b	90.6 a
27 Oct 92	22.6 b	2.1 c	24.8 b	90.4 a

[1]Each mean is based on ten trees. Means were compared using Duncan's multiple range test at the 5% level. Means in each column that are followed by the same letter are not significantly different.

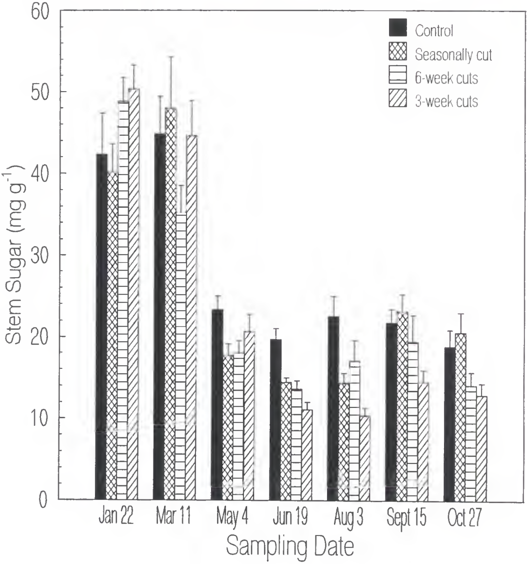

Figure 9. Variations in stem sugar concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

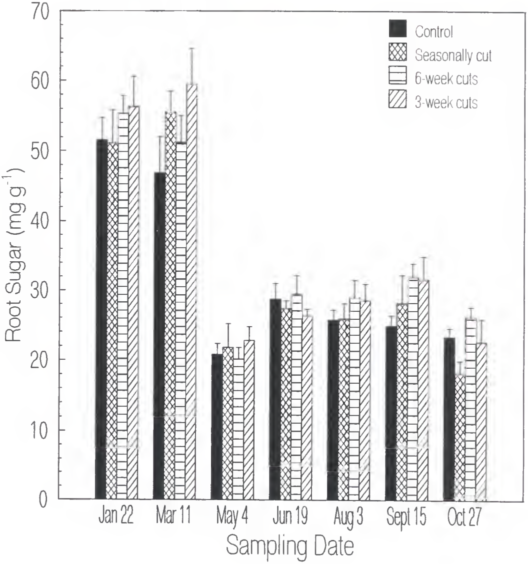

Figure 10. Variations in root sugar concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

the subsequent five sampling dates (May 4 through October 27). Dry-season sugar concentrations were roughly twice as large as wet-season concentrations.

In all treatments, sugar concentrations were significantly higher in the roots than in the stems (Table 23). As in the gliricidia study, the magnitude of the difference between stem sugar and root sugar was increased by frequent cutting. In the uncut control the difference was approximately 4 mg g^{-1}, while in the 3-week treatment it was 12 mg g^{-1}.

Starch. Analysis of covariance (all sampling dates combined) revealed significant treatment effects for starch (Table 16). As with gliricidia, starch concentrations in both stems and roots decreased as cutting frequency increased. In stems, starch concentrations in all three cutting treatments were significantly lower than those in the control. For starch concentrations in roots, the control was significantly higher than all other treatments, and the seasonally cut treatment was significantly higher than the 3-week treatment and 6-week treatment.

Analysis of samples collected on individual sampling dates also revealed significant treatment effects for stem and root starch (Tables 17 and 18, Figures 11 and 12). In stems, the initial cut decreased starch in the three cutting treatments to approximately one-third that in the control.

Table 23. *Leucaena leucocephala*: Within-treatment comparisons of root and stem carbohydrates.

Treatment[1]	Plant Component	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total (mg g^{-1})
1	Root	31.7 a	28.1 a	59.9 a
	Stem	27.8 b	18.0 b	45.8 b
2	Root	32.5 a	17.7 a	50.2 a
	Stem	25.6 b	9.1 b	34.8 b
3	Root	34.8 a	11.8 a	46.6 a
	Stem	23.6 b	5.6 b	29.2 b
4	Root	35.3 a	9.7 a	45.0 a
	Stem	23.3 b	6.7 b	30.0 b

[1]Treatment 1 = uncut control; Treatment 2 = cut twice; Treatment 3 = cut at 6-week intervals; Treatment 4 = cut at 3-week intervals.

[2]Each mean is based on 70 trees, ten from each of seven sample dates. Means were compared using t-tests of least squares means at the 5% level. Means in each sampling group (same treatment and carbohydrate variable) that are followed by the same letter are not significantly different.

This was the quickest response to cutting—and the only dry-season response—noted in either the gliricidia or leucaena study. For five sampling dates (March 11 through September 15), stem starch in the control was significantly higher than in all other treatments. The seasonally cut treatment was significantly higher than the 3-week and 6-week treatments on June 13 and August 3. On October 27, stem starch in the seasonally cut treatment rose, while that in the control dropped. On this date, stem starch was significantly higher in the seasonally cut treatment than in the 3-week and 6-week treatments; the control was not significantly different from any other treatment.

For root starch, in general, there was high variability of values in the samples (as indicated by the error bars in Figure 12). Significant treatment effects first surfaced on May 4, the third sampling date and first wet-season date. On May 4, June 19, and September 15, the control was significantly higher than all other treatments. On August 3 and October 7, both the control and the seasonally cut treatment were significantly higher than the 3-week and 6-week treatments.

Within-treatment comparisons of stem starch concentrations over time revealed rapid effects of cutting (Tables 19-22). On March 11—the first sampling date after the initial cut—stem starch concentrations in the 3-week

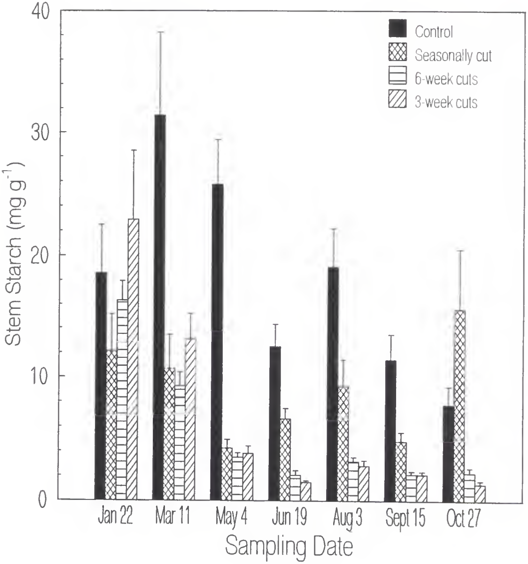

Figure 11. Variations in stem starch concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

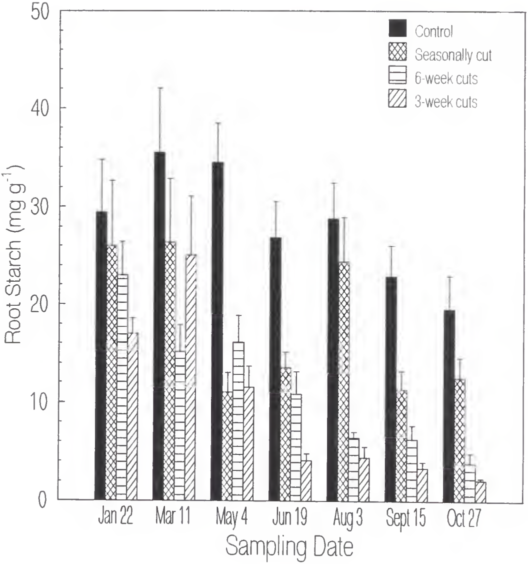

Figure 12. Variations in root starch concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

and 6-week treatments were significantly lower than pre-cutting levels (i.e., January 22). Stem starch concentrations in these two treatments continued to decrease until the next sampling date (May 4), and then stabilized at levels that were approximately 20% of the pre-cutting concentration. On the five sampling dates from May 5 through October 27 stem starch concentrations in the 3-week and 6-week treatments were significantly lower than those of January 22 and March 11.

Results in the seasonally cut treatment were not as well defined as those in the 3-week and 6-week treatments. In this treatment, the highest stem starch concentration (15.6 mg g^{-1}) was recorded on October 27, the last sampling date (Table 20). Only the October 27 and May 4 sampling dates were significantly different. Nevertheless, except for October 27, the trend in the seasonally cut treatment resembles that in the two frequently cut treatments. A large decrease in stem starch was noted on the first wet-season sampling date (May 4), and then levels remained relatively low, although not as low as in the 3-week and 6-week treatments.

In the control, stem starch concentrations were at a low of 7.7 mg g^{-1} on October 27 (the seasonally cut treatment's peak) and reached a high of 31.4 mg g^{-1} on March 11 (Table 19). Stem starch concentrations for March 11 were significantly higher than those for June 19, September 15,

and October 27. May 4 was also significantly higher than October 27.

Within-treatment comparisons of root starch over time revealed patterns similar to those observed in stem starch, i.e., starch concentrations decreased with cutting (Tables 19-22). However, the effects were not so clearly defined as in stem starch. In the 3-week and 6-week treatments, root starch gradually decreased as the cutting treatments progressed, but changes occurred more slowly than in the stems. The decrease was also slower in the 6-week treatment than in the 3-week treatment. In the 3-week treatment, the last five sampling dates (May 4 through October 27) were significantly lower than March 11, and the last four dates were significantly lower than January 22. On the last four dates, root starch values were very similar to stem starch values from the same period. In the 6-week treatment, the four dates from June 19 through October 27 were significantly lower than January 22; September 15 and October 27 were significantly lower than May 4; and October 27 was significantly lower than March 11. Values during the last three sampling dates were only slightly higher than the low values reported for the 3-week treatment.

In the control and the seasonally cut treatment, no date was significantly different from another for root starch concentrations. However, trends in root starch tended to follow the trends observed for stem starch. In

the control, root starch was highest on March 11 and May 4 (approximately 35 mg g^{-1}) and lowest on October 27 (19.5 mg g^{-1}). In the seasonally cut treatment, root starch concentrations on January 22, March 11, and August 3 were twice as large as those from the other four sampling dates.

In all treatments, root starch (all dates combined) was significantly higher than stem starch (Table 23). Mean starch concentrations in stems ranged from 5.6 mg g^{-1} in the 6-week treatment to 18.0 mg g^{-1} in the control. In roots, concentrations ranged from 9.7 mg g^{-1} in the 3-week treatment to 28.1 mg g^{-1} in the control.

Unlike sugar and starch in gliricidia, and sugar in leucaena, the difference between levels of stem- and root starch in leucaena was not clearly increased by frequent cutting. In the uncut control, root starch concentration was approximately 1.6 times higher than stem starch concentration; in the seasonally cut treatment 2.0 times higher; and in the 6-week treatment 2.1 times higher. In the 3-week treatment, however, root starch was only 1.4 times higher than stem starch; i.e., the most frequently cut treatment had the smallest difference between stem starch and root starch. In that treatment, both stem- and root starch had been quickly reduced to near-depletion levels.

Starch concentrations in leucaena were considerably lower than those in gliricidia (Tables 2, 3, 17, 18). In the leucaena control, mean stem starch (all sampling dates

combined) was 18.0 mg g^{-1} and mean root starch was 28.1 mg g^{-1}. Comparable values in gliricidia were 41.1 mg g^{-1} and 158.6 mg g^{-1}.

Total reserve carbohydrates. Analysis of covariance of all sampling dates combined revealed significant treatment effects for total reserve carbohydrates in both stems and roots (Table 16). In both plant parts, the control had a significantly higher concentration of reserve carbohydrates than the three cutting treatments. There was no difference in total reserve carbohydrate concentrations among the seasonally cut, 3-week, and 6-week treatments.

As in the gliricidia study, cutting altered the composition of reserve carbohydrates (as indicated by sugar percent of total reserve carbohydrates) (Table 24). Stem sugar percentage was significantly higher in the 3-week and 6-week treatments than in the control and seasonally cut treatment, and significantly higher in the seasonally cut treatment than in the control. In roots, all four treatments were significantly different with respect to sugar percentage; values increased as cutting frequency increased.

When sampling dates were examined individually, significant treatment effects were revealed for both stem and root reserve carbohydrates (Tables 17 and 18, Figures 13 and 14). On March 11 (the first post-cutting sampling date), total stem reserve carbohydrates in the 6-week

treatment were significantly lower than in the control. On May 4, June 19, and August 3, the control was significantly higher than all other treatments; on September 15, it was significantly higher than the 3-week and 6-week treatments; and on October 27, it was significantly higher than the 3-week treatment. The seasonally cut treatment was significantly higher than the 3-week treatment on June 19, August 3, and September 15; and significantly higher than the 3-week and 6-week treatments on October 27.

In general, total stem carbohydrates in leucaena followed the trend observed in gliricidia, i.e., cutting reduced carbohydrate concentrations. However, the two species differed in that all three cutting treatments in gliricidia had similar total stem carbohydrate concentrations on all sampling dates; in leucaena, after treatment effects appeared, concentrations in the seasonally cut treatment were generally significantly higher than one or both of the more frequently cut treatments.

For total root carbohydrates, significant effects were first noted on May 4 (the first wet-season sampling date). The control was significantly higher than all other treatments on May 3, June 19, and October 27; significantly higher than the 3-week and 6-week treatments on August 3; and significantly higher than the 3-week treatment on September 15. The seasonally cut treatment was

Table 24. *Leucaena leucocephala*: The effect of pruning frequency on the composition of reserve carbohydrates

Treatment[1]	Stem Sugar[2] (%)	Root Sugar (%)
1	62.4 c	53.4 d
2	74.3 b	65.3 c
3	83.1 a	76.8 b
4	82.1 a	81.7 a

[1]Treatment 1: uncut control; Treatment 2: cut twice; Treatment 3: cut at 6-week intervals, a total of 6 cuts; Treatment 4: cut at 3-week intervals, a total of 11 cuts.

[2] Expressed as a percentage of total reserve carbohydrates. Each mean is based on 70 trees, ten from each of seven sample dates (n=70). Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different.

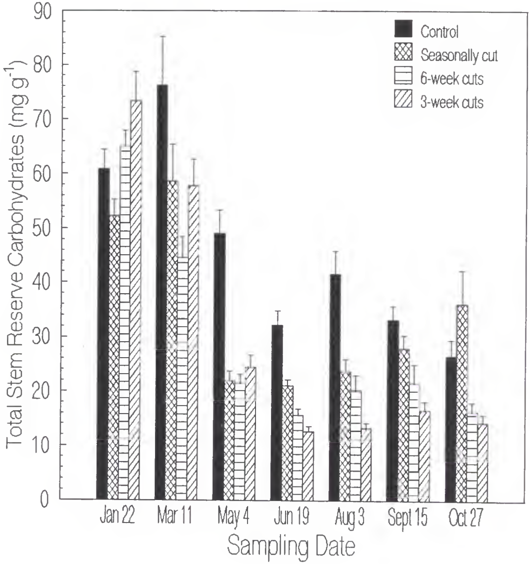

Figure 13. Variations in total stem carbohydrate concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

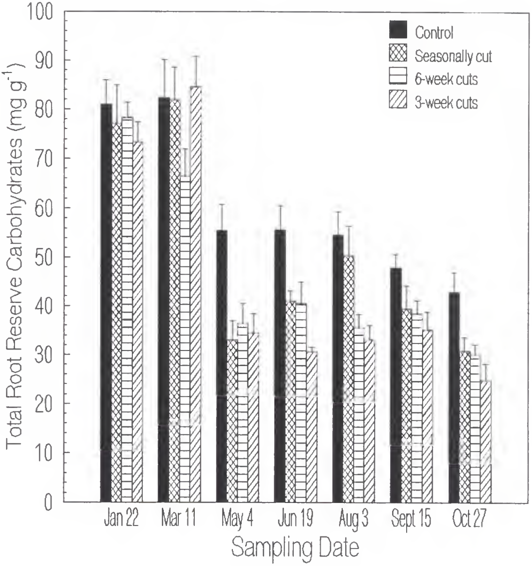

Figure 14. Variations in total root carbohydrate concentrations in *Leucaena leucocephala*, January to October, 1992. Each bar is the mean of 10 observations. Lines on top of bars signify one standard error.

significantly higher than the 3-week and 6-week treatments on August 3.

Within-treatment comparisons of total reserve carbohydrates in both stems and roots revealed significant time effects (Tables 19-22). In general, total reserve carbohydrate concentrations in both stems and roots were higher on the two dry-season sampling dates (January 22 and March 11) than on the five wet-season dates (May 4 through October 27).

In the control, total stem carbohydrates on March 11 were significantly higher than those on all sampling dates except January 22; January 22 concentrations were significantly higher than those on June 19, September 15, and October 27; and May 4 concentrations were significantly higher than those on October 27. Values ranged from a March peak of 76.2 mg g^{-1} to an October low of 26.6 mg g^{-1}. The effect of season on total stem carbohydrates seemed to be stronger in leucaena than in gliricidia, which had relatively stable stem carbohydrate concentrations in the control, except for a June/July decrease.

In the seasonally cut treatment, total stem carbohydrate concentrations on March 11 were significantly higher than those on all sampling dates except January 22, and concentrations on January 22 were significantly higher than on the four dates from May 4 through September 15.

Within-treatment comparisons in the 3-week and 6-week treatments revealed that total stem carbohydrates on January 22 were significantly higher than on all other sampling dates, and concentrations on March 11 were significantly higher than on the succeeding five dates from May 4 through October 27.

With regard to total root carbohydrates, all four treatments exhibited the same trend. The two dry-season dates (January 22 and March 11) were significantly higher than the five wet-season dates (May 4 through October 27). In the control, total root carbohydrate values ranged from 81-82 mg g^{-1} in January and March to 42.8 mg g^{-1} on October 27. As with total stem carbohydrates, the effect of season on total root carbohydrates was apparently stronger in leucaena than in gliricidia. Both sugar and starch concentrations decreased during the wet season, but sugar experienced the greatest decline, so contributed most to the lower total carbohydrate concentrations.

In all treatments, total root carbohydrates (all dates combined) were significantly higher than total stem carbohydrates (Table 23). The magnitude of the difference between stem and root carbohydrate concentrations in leucaena was approximately half as large as in gliricidia. In leucaena, root carbohydrate concentrations were between 1.3 and 1.6 times larger than stem concentrations.

Dry matter production

Treatment effects. Cumulative dry matter production during the leucaena study—January 24, 1992 to December 8, 1992—was 566 g $tree^{-1}$ in the seasonally cut treatment (3 cuts), 119 g $tree^{-1}$ in the 6-week treatment (7 cuts), and 54 g $tree^{-1}$ in the 3-week treatment (12 cuts). All treatment means were significantly different (Table 25).

The leucaena study included only the second half of the long dry season (January 24 to March 16). All three cutting treatments were cut at the beginning of this period and again at its end. For this cutting interval, no treatment was significantly different from another with regard to biomass production. Treatment means ranged from 9.7 g $tree^{-1}$ to 11.6 g $tree^{-1}$ (Table 25).

During the wet season (March 16 to October 28), all three cutting treatments were significantly different in cumulative biomass production (Table 25). Dry matter production decreased as cutting frequency increased. During this period, the seasonally cut treatment (1 cut) produced 539 g $tree^{-1}$, the 6-week treatment (5 wet-season cuts) produced 101 g $tree^{-1}$, and the 3-week treatment (10 wet-season cuts) produced 39 g $tree^{-1}$.

Only the 3-week and 6-week treatments were cut at regular intervals during the entire study period. Therefore, only these two treatments were compared for dry matter production during individual growth intervals (Table

26). During the two sampling intervals (March 16 and December 8 sampling dates) when these treatments received the same number of cuts, their dry matter production was not significantly different. However, when the 3-week treatment was cut twice during a 6-week growth interval, this treatment produced significantly less biomass (cumulative production from two 3-week growth intervals) than the 6-week treatment.

Within-treatment comparisons of dry matter production during different growth intervals, in the 3-week and 6-week treatments, revealed significant differences among sampling dates (Tables 27 and 28). In the 3-week treatment, the greatest dry matter production occurred during the first wet-season growth interval (May 6 sampling date). Production increased from 10 g $tree^{-1}$ on March 16 (1 cut) to 16 g $tree^{-1}$ on May 6 (aggregate of 2 cuts). In the 6-week treatment, the greatest dry matter production occurred during the second wet-season growth interval (June 22 sampling date). Production increased from 12 g $tree^{-1}$ on March 16 to 25 g $tree^{-1}$ on May 6, and then to 32 g $tree^{-1}$ on June 22. The peak biomass values in both treatments were significantly higher than those of all other sampling dates.

From the peak values, dry matter production in leucaena steadily decreased in both treatments. In the 6-week treatment, dry matter production on the four sampling dates from August 4 through December 8 decreased from 19 g $tree^{-1}$

Table 25. *Leucaena leucocephala*: Seasonal and cumulative dry matter production in the cutting treatments.

Sample Period	Trt	Number of cuts to date[1]	Mean production[2] (g $tree^{-1}$)	Mean daily productivity (g $tree^{-1}$ day^{-1})
Dry Season:	2	1	9.7 a	0.19
24 January	3	1	11.6 a	0.22
to 16 March	4	1	9.9 a	0.19
Wet Season:	2	2	539.1 a	2.38
16 March	3	6	100.8 b	0.45
to 28 October	4	11	38.7 c	0.17
28 October	2	3	17.4 a	0.43
to	3	7	6.8 b	0.17
8 December	4	12	5.3 b	0.13
Total:	2	3	566.2 a	1.78
24 January	3	7	119.2 b	0.37
to 8 December	4	12	53.8 c	0.17

[1]Number of cuts refers to the total number of times trees were pruned prior to, but not including, the end date of a sample period.

[2]Means were compared using Duncan's multiple range test at the 5% level. Means for each sample period are not significantly different when followed by the same letter.

Table 26. *Leucaena leucocephala*: Comparisons of dry matter production in the 3-week and 6-week treatments, from 24 January 1992 to 8 December 1992.

Harvest Date	Trt[1]	Number of cuts to date	Mean production[2] (g tree^{-1})	Mean daily productivity (g tree^{-1} day^{-1})
16 Mar	3	1	11.6 a	0.22
	4	1	9.9 a	0.19
6 May	3	2	24.9 a	0.49
	4	3	15.6 b	0.31
22 Jun	3	3	31.8 a	0.68
	4	5	10.3 b	0.22
4 Aug	3	4	19.2 a	0.45
	4	7	5.3 b	0.12
17 Sep	3	5	14.0 a	0.32
	4	9	4.1 b	0.09
28 Oct	3	6	10.9 a	0.26
	4	11	3.4 b	0.08
8 Dec	3	7	6.8 a	0.17
	4	12	5.3 a	0.13

[1]Treatment 3 = 6-week cutting interval; Treatment 4 = 3-week cutting interval.

[2]Means were compared using t-tests of least square means ($P \leq 0.05$). Means at each date are significantly different when followed by different letters. Treatment 3 means are based on 90 trees; treatment 4 means are based on 170 trees. Treatment 4 dry matter production is the sum of two cuts, except during the 16 March and 8 December sample periods when trees were cut only once.

Table 27. *Leucaena leucocephala*: Dry matter production in the 6-week treatment, from 24 January 1992 to 8 December 1992.

Harvest date	Mean cumulative production[1] (g $tree^{-1}$)	Mean daily productivity (g $tree^{-1}$ day^{-1})
16 Mar	11.6 d	0.22 de
6 May	24.9 b	0.49 b
22 Jun	31.8 a	0.68 a
4 Aug	19.2 c	0.45 b
17 Sep	14.0 d	0.32 c
28 Oct	10.9 d	0.26 cd
8 Dec	6.8 e	0.17 e

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 5 plots, with 18 trees per plot.

Table 28. *Leucaena leucocephala*: Dry matter production in the 3-week treatment, from 24 January 1992 to 8 December 1992.

Harvest date	Mean cumulative production[1] (g $tree^{-1}$)	Mean daily productivity (g $tree^{-1}$ day^{-1})
16 Mar[2]	9.9 b	0.19
6 May	15.6 a	0.31
22 Jun	10.3 b	0.22
4 Aug	5.3 c	0.13
17 Sep	4.1 cd	0.09
28 Oct	3.4 d	0.08
8 Dec[2]	5.3 c	0.12

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Unless otherwise noted, dry matter is the production from two cuts during the sample period. Means are based on 5 plots, with 34 trees per plot.

[2]Dry matter is the production from one cut.

to 7 g $tree^{-1}$. Values from the August 4 sampling date were significantly higher than those from September 17, October 28, and December 8. Production on September 17 and October 28 was significantly higher than on December 8. In the 3-week treatment, dry matter production (aggregate of 2 cuts) on the four sampling dates from June 22 through October 28 gradually dropped from 10 g $tree^{-1}$ to 3 g $tree^{-1}$. June 22 value was significantly higher than August 4, September 17, and October 28 values. The August 4 value was significantly higher than that of October 28.

For both treatments, the lowest dry matter production (for a growth interval with six weeks of uninterrupted growth) occurred during the last growth interval (December 8 sampling date). This contrasts with gliricidia, which produced the least biomass during the first growth interval. For the 6-week treatment, the December 8 value (7 g $tree^{-1}$) was significantly lower than the means from all other sampling dates. For the 3-week treatment, dry matter production from December 8 (5 g $tree^{-1}$) was significantly lower than production from May 6 and June 22, and not significantly different from production from August 4 and September 17. It needs to be noted that biomass on the May 6 through September 17 sampling dates was the aggregate of two cuts, while biomass on December 8 was from a single cut.

For samples collected on October 28, biomass was sorted into leaves and stems, and the mean dry weight of each

component was calculated separately. At that time, control trees had not been cut since the end of 1990, and trees in the seasonally cut treatment had not been cut for approximately 32 weeks. Trees in the 6-week treatment had six weeks of growth; those in the 3-week treatment had three weeks of growth. Mean tree biomass (n=10) in the control was 714 g $tree^{-1}$, in the seasonally cut treatment 612 g $tree^{-1}$, in the 6-week treatment 11 g $tree^{-1}$, and in the 3-week treatment 2 g $tree^{-1}$. Mean comparisons of the four treatments revealed that the 3-week and 6-week treatments were significantly different from the other two treatments. Because the large disparity between means from the frequently cut treatments and those from other two treatments could hide significant differences, pair-wise comparisons were also performed. These revealed that the 3-week treatment and 6-week treatment were significantly different, but the control and seasonally cut treatment were not.

The proportion of total dry matter in the October samples that was composed of leaves varied considerably among treatments. In the control, leaf dry matter accounted for 12.4% of total aboveground biomass; in the seasonally cut treatment 17.1%; in the 6-week treatment 56.9%; and in the 3-week treatment 71.6%, all differences being significant.

Dry matter production as function of carbohydrate concentrations. The association between dry matter production and reserve carbohydrates in the 6-week and 3-week treatments during the wet season was evaluated using linear regression and correlation analysis. For the analysis, mean dry matter production and mean carbohydrate concentrations were calculated for each of five growth intervals (n=5), which ended on the May 6, June 22, August 4, September 17, and October 28 sampling dates. Each biomass mean was based on the production of 170 trees (34 trees per plot) in the 3-week treatment, and 90 trees (18 trees per plot) in the 6-week treatment. Each carbohydrate mean was based on ten trees (2 trees per plot). Analyses used carbohydrate values from the beginning of a growth interval and biomass values from the end.

Correlation analysis revealed a significant linear association ($P \leq 0.05$) between dry matter production and several of the reserve carbohydrate variables (Table 29). In the 6-week treatment, significant correlations were found between dry matter and root starch, and dry matter and root sugar percentage. In the 3-week treatment, significant correlations were found between dry matter and stem sugar, stem starch, total stem carbohydrates, and root starch. Figure 15 presents regressions of wet-season dry-matter production against root starch in the 3-week and 6-week treatments.

All cutting treatments were harvested on October 28, and were then allowed to grow undisturbed until December 8, 1992, when they were cut again (Table 25). Correlation analysis, which included all three cutting treatments, revealed significant linear correlations between plot means for dry matter production and reserve carbohydrates for this growth interval (Table 30). Results of this analysis were similar to results listed in Table 29 for the 3-week and 6-week treatments during the wet season. For the October-to-December biomass production, however, more correlations were significant, possibly because of the higher degrees of freedom (n=15).

Table 29. *Leucaena leucocephala*: Correlation coefficients for dry matter as a linear function of reserve carbohydrate concentrations in the 3-week and 6-week treatments.

Y variable	X variable	Correlation Coefficient[1] (r)	
		Treatment[2] 3	Treatment[2] 4
Dry Matter ($g\ tree^{-1}$)	Stem Sugar	0.28 ns	0.93 *
	Stem Starch	0.43 ns	0.89 *
	Stem Total	0.32 ns	0.92 *
	Stem Sugar %	-0.60 ns	-0.45 ns
	Root Sugar	-0.06 ns	0.71 ns
	Root Starch	0.97 **	0.97 **
	Root Total	0.29 ns	0.84 ns
	Root Sugar %	-0.89 *	-0.88 ns

[1]Each correlation is based on means from five sample dates between May 1992 and October 1992 (n=5); only wet-season dates were included. Reserve carbohydrate concentrations ($mg\ g^{-1}$) were measured at the beginning of each growth interval. Dry matter was measured at the end of each growth interval.

[2]Treatment 3 = 6-week cutting interval; Treatment 4 = 3-week cutting interval.

Table 30. *Leucaena leucocephala*: Correlation coefficients for dry matter as a linear function of reserve carbohydrate concentrations for the period from 28 October 1992 to 8 December 1992.

Y variable	X variable	Correlation Coefficient[1] (r)
Dry Matter (g $tree^{-1}$)	Stem Sugar	0.65 **
	Stem Starch	0.75 **
	Stem Total	0.79 ***
	Stem Sugar %	-0.83 ***
	Root Sugar	-0.51 ns
	Root Starch	0.93 ***
	Root Total	0.39 ns
	Root Sugar %	-0.94 ***

[1]Each correlation is based on fifteen plot means, five from each cutting treatment (n=15). Reserve carbohydrate concentrations (mg g^{-1}) were measured at the beginning of the growth interval. Dry matter was measured at the end of the growth interval.

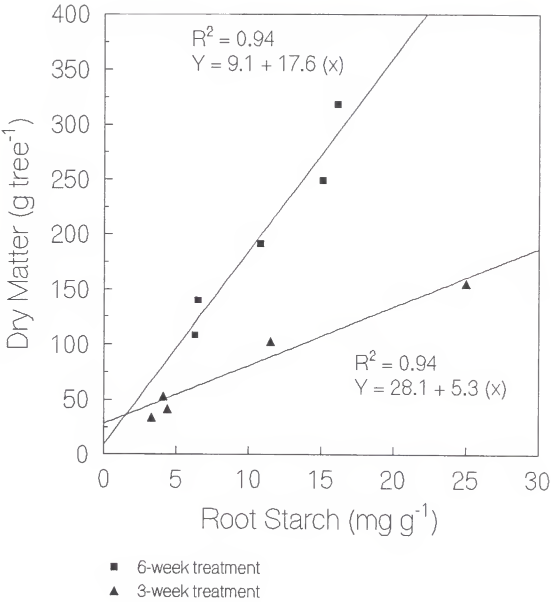

Figure 15. Regression of dry matter on root starch in the 3-week and 6-week treatments. Each point is based on means for a wet-season sampling date from May to October, 1992.

Discussion

Reserve Carbohydrate Concentrations

As detailed in the Literature Review (Chapter 2), numerous studies have reported that reserve carbohydrates in temperate woody plants decrease as regrowth occurs after cutting, burning or defoliation. The same trend has been reported in the few tropical species that have been investigated (Nagarajah & Pethiyagoda, 1965; Selvendran & Selvendran, 1972; Kandiah et al., 1984; Miyanishi & Kellman, 1986; Erdmann et al., 1993; Rodgers et al., 1995). Additionally, for both temperate and tropical species, it has been noted that reserve carbohydrate depletion is worsened when trees are cut or defoliated repeatedly at short intervals (Bamber & Humphreys, 1965; Wargo et al., 1972; Miyanishi & Kellman, 1986; Harrington, 1989). Results from the present study agree with these earlier reports.

Effect of cutting on reserve carbohydrate concentrations

Cutting decreased mean starch and total reserve carbohydrate concentrations in both stems and roots of gliricidia and leucaena (Tables 1 and 16). In general, carbohydrate levels decreased as frequency of cutting increased, although treatments were not always significantly different. Reductions were most severe in the two most frequently cut treatments. In gliricidia, the 6-week and 3-week treatments had significantly lower mean starch

concentrations in roots and stems than either the uncut control or the seasonally cut treatment. In leucaena, all three cutting treatments had significantly lower starch levels in stems and roots than did the control. Total reserve carbohydrate concentrations in both roots and stems in leucaena, and stems in gliricidia, were significantly lower in the three cutting treatments than in the uncut control. In gliricidia roots, the highest concentrations of total reserve carbohydrates were also observed in the control, but levels were significantly different only from the 3-week treatment. All of these results conform to the expected trend.

It was also expected that the two most frequently cut treatments would have significantly lower concentrations of total reserve carbohydrates than the seasonally cut treatment. Interestingly, that was not the case when data from all sampling dates were combined (Tables 1 and 16). Mean total reserve carbohydrate levels in the three cutting treatments were not significantly different. This was true in both species, and in both roots and stems. When sampling dates were considered individually, however, the seasonally cut treatment was occasionally significantly higher than one or both of the more frequently cut treatments (Figures 6, 7, 13, 14; Tables 2, 3, 17, 18). Only in leucaena stems were higher values in the seasonally cut treatment a persistent trend.

Cutting, however, altered the proportions of sugar and starch. Sugar percentage of total reserve carbohydrates was increased by frequent cutting (Tables 9 and 24). In the 3-week and 6-week treatments (both species, roots and stems) this value was generally twenty to thirty percentage points higher than in the uncut control. Sugar percentages in the seasonally cut treatment were usually intermediate to those in control and frequently cut trees. These results lead to the conclusion that repeated cutting and regrowth cause plants to maintain more of their carbohydrate reserves as readily transportable and usable sugars. Starch reserves are hydrolyzed to ensure an adequate supply of sugars for regrowth and other plant needs. This leads to the progressive reduction of starch reserves, while sugar concentrations are maintained at, or above, normal levels. Starch-sugar conversions are common in woody plants (Kramer & Kozlowski, 1979). Starch is transformed to sugars whenever sugar levels are low (Kozlowski & Keller, 1966).

The effect of cutting on soluble sugar levels was quite different in gliricidia and leucaena. In gliricidia, there were large and significant differences between the 6-week and 3-week treatments, and the other two treatments (Figures 2, 3; Tables 1, 2, 3). This difference was most pronounced in the roots. In roots, sugar levels in the 6-week and 3-week treatments increased steadily as the experiment progressed. By the end of the study, root sugar levels in

the frequently cut treatments were more than three times higher than levels in the other two treatments. In contrast, gliricidia stems did not experience an increase in sugar. Rather, sugar levels in the two frequently cut treatments were maintained at the high dry-season levels, while concentrations in the other treatments decreased in accordance with normal seasonal trends. In leucaena, there were no significant treatment effects for sugar (Figures 9, 10; Tables 16, 17, 18).

It seems likely that the size of starch stores in gliricidia and leucaena influenced sugar levels in the frequently cut treatments. In roots, starch concentrations in gliricidia were approximately 5.5 times higher than in leucaena; in stems, concentrations in gliricidia were about twice as high as in leucaena (Tables 1 and 16). The large supply of starch may have allowed gliricidia to maintain sugar at higher-than-normal levels in the frequently cut treatments. On the other hand, starch reserves in leucaena were quickly depleted so could not support high sugar levels.

This study did not investigate changes in the types of soluble carbohydrates found in roots and stems after cutting, but such changes can be considerable. Tschaplinski and Blake (1994) found that sucrose concentrations in roots of cut poplar decreased, while concentrations of glucose and fructose increased. This increase was followed by the

accumulation of shikimic acid, salicyl alcohol, unknown compound A, and salicin.

Source of reserve carbohydrates used during regrowth after cutting

The relative importance of carbohydrate stores in stems and roots for regrowth after cutting probably depends on the species under consideration. Many studies have stressed the importance of root reserves. Examples include sugar maple (*Acer saccharum*) (Wargo et al., 1972), pecan (*Carya illinoensis*)(Worley, 1979), *Citrus* (Eissenstat & Duncan, 1992), *Quercus gambelii* (Harrington, 1989), sweetgum (*Liquidamber styraciflua*) (Wenger, 1953), desert shrubs (Trlica & Cook, 1971), *Eucalyptus* spp. (Taylor et al., 1982), *Cedrela odorata* (Rodgers et al., 1995), and tea (*Camellia sinensis*) (Kandiah, 1971). A number of studies have also reported decreases in stem starch in severely defoliated plants, for example, gliricidia (Erdmann et al., 1993), *Quercus velutina* (Parker & Patton, 1975), *Populus* hybrids (Tschaplinski & Blake, 1994), and *Pseudotsuga menziesii* (Webb & Karchesy, 1977). Loescher et al. (1990) noted that in apple the distribution of carbohydrates between above-ground and below-ground tissues remained constant even though the total amount in the tree fluctuated. The implication was that reserve carbohydrates in stems and roots provide equal support to shoot growth. It has also been reported that during growth, woody plants

initially use carbohydrate stores that are located closest to the site of utilization (Kozlowski & Keller, 1966).

Results from the present study indicate that post-cutting biomass production in gliricidia and leucaena uses starch reserves in both stems and roots. Coppice sprout production is supported first by stem starch reserves, and later by root starch reserves (Figures 4, 5, 11, 12; Tables 2, 3, 17, 18). Erdmann et al. (1993) also reported that resprouting in gliricidia is initially supported by stem starch. In gliricidia, stem starch levels in all three cutting treatments were significantly reduced on the fourth sampling date (April 30), at the end of the first wet-season growth interval. Definite treatment effects in gliricidia roots did not appear until the next sampling date—June 16. At that time, root starch was significantly reduced in the 6-week and 3-week treatments (4 cuts and 6 cuts). Starch reductions after cutting appeared more quickly in leucaena, but again, stem starch decreased first. After one cut (January 22), stem starch in leucaena was significantly reduced in the three cutting treatments. Root starch also may have decreased at this time but the reduction was not as large as in stems, and significant treatment differences were not observed until the next sampling date.

Comparison of reserve carbohydrate concentrations in stems and roots

In their extensive review of reserve carbohydrates in woody roots, Loescher et al. (1990, p. 275) state that, "...regardless of species or flowering and fruiting behavior, the root system nearly always contains higher concentrations of nonstructural carbohydrates than any other portion of the tree, and therefore has been considered the main site of carbohydrate storage." The Literature Review (p. 7) cites numerous references that support this assertion. Results from the present study also conform to this trend (Tables 8 and 23). For both species and all treatments, starch and total reserve carbohydrate concentrations were significantly higher in roots than in stems. For all leucaena treatments and the three gliricidia cutting treatments, sugar concentrations in the roots were also significantly higher than in the stems. In the gliricidia control, stem and root sugar concentrations were not significantly different.

In general, the magnitude of the difference between stem reserves and root reserves was increased by cutting. For example, in the uncut gliricidia control, starch concentrations in roots were approximately four times higher than in stems, while in the three cutting treatments, root starch was approximately six times higher. This occurred because stem carbohydrates decreased more quickly than root

carbohydrates after cutting. However, if frequent cutting continues for an extended period, carbohydrates in both stems and roots can approach near-depletion levels. Obviously, when this occurs, differences between root and stem carbohydrate concentrations will no longer exist. This trend was observed in leucaena. In leucaena roots, starch concentrations in the control were 1.6 times higher than in stems, in the seasonally cut treatment 2.0 times higher, in the 6-week treatment 2.1 times higher, and in the 3-week treatment 1.4 times higher. By the end of the study period, starch concentrations in both stems and roots of the 3-week treatment had been reduced to 1 to 2 mg g^{-1} (Table 17 and 18). It would be expected that, had cutting continued, the same results would have appeared in the 6-week treatment as well.

Depletion of reserve carbohydrates and mortality

Repeated destruction of above-ground biomass can result in significant mortality in woody plants (Christensen & Kimber, 1975; White, 1983; Miyanishi & Kellman, 1986; Strong, 1989). Depletion of reserve carbohydrates as a result of frequent resprouting probably contributes to increased mortality. Studies of reserve carbohydrate levels during different seasons and following shoot destruction have found that the highest mortality (and least sprouting) coincided with low carbohydrate levels (Jones & Laude, 1960; Laude et al., 1961; Wright & Stinson, 1970; Leege & Hickey,

1971; Trlica & Cook, 1971; Gregory & Wargo, 1986; Miyanishi & Kellman, 1986; Harrington, 1989; Kays & Canham, 1991).

Starch reserves seem to be of particular relevance. Starch is the main form in which most plants store carbohydrates; when levels of soluble carbohydrates are inadequate to meet a plant's requirements, starch is hydrolyzed to sugars. Therefore, starch is often used as the sole indicator of a plant's reserve carbohydrate status (Ford & Deans, 1977; Adams et al., 1986). There is also evidence that starch may contribute more to a plant's resprouting ability than other compounds that could be reduced by frequent cutting. Miyanishi and Kellman (1986) evaluated the effect of repeated burning on levels of Ca, Mg, K, P, and starch in the roots of two tropical savanna shrubs. Only starch was significantly decreased by top kills, and was therefore identified as the most likely variable to limit resprouting.

A number of studies have reported the ability of gliricidia and leucaena to withstand repeated cuttings (Kang et al., 1985; Budelman, 1987; Attah-Krah & Sumberg, 1988; Ella et al., 1989; Ella et al., 1991). This ability was also noted in the present study. No mortality occurred in the gliricidia experiment, even after thirteen cuts in less than 11 months in the 3-week treatment. In the leucaena experiment, five trees in the 3-week treatment died after the October, 1992 cut. This mortality occurred after twelve

cuts, and after starch reserves in stems and roots had declined to near-depletion levels. On the October 27 sampling date, stem starch in this treatment was 1.4 mg g^{-1}, and root starch was 2.1 mg g^{-1} (Tables 17 and 18). In comparison to the control, stem starch was decreased 82% and root starch was decreased about 90%. It should be noted that control trees were fruiting on this date, which reduced their starch levels. Comparisons with non-fruiting trees probably would have shown greater relative depletion in the frequently cut trees. Additionally, the above percentages are based on mean concentrations in the 3-week treatment. The dead trees might have had lower starch levels. The lowest values I recorded on this date were 0.36 mg g^{-1} in stems and 1.2 mg g^{-1} in roots. Miyanishi and Kellman (1986) found that root starch was almost completely depleted (97—98%) in *Miconia albicans* and *Clidemia sericea* shrubs that failed to resprout after multiple shoot removals.

Reserve carbohydrate concentrations in gliricidia were much higher than those in leucaena, and this may have prevented mortality in the gliricidia experiment. In the gliricidia control, mean stem starch was 38.9 mg g^{-1} and root starch 158.6 mg g^{-1} (Table 1). In the leucaena control, mean stem starch was 18.0 mg g^{-1} and root starch was 28.1 mg g^{-1} (Table 16). Even in the most frequently cut gliricidia trees, carbohydrate reserves were far from depleted (Tables 2 and 3). Although stem starch concentrations in the 6-week

and 3-week treatments in gliricidia decreased almost to the levels observed in leucaena, root starch concentrations at their lowest (approximately 60 mg g^{-1}) were much higher than in leucaena.

These observations suggest that mean reserve carbohydrate levels in different species might be useful indicators of a species' tolerance of frequent cutting. However, this is only partially true. Even with much lower reserve carbohydrate levels than gliricidia, leucaena proved to be very tolerant of frequent cutting. In the long run, carbohydrate reserves in any species will be depleted by frequent cuts unless adequate time is allowed for replenishment.

Rate of reserve carbohydrate replenishment

Coppice shoots may quickly become self-sufficient with regard to carbohydrates, so replenishment of reserve carbohydrate stores might begin fairly soon after cutting (Priestley, 1963; Hansen, 1971, Kandiah, 1971; Kandiah et al., 1984). Priestley (1963) found that carbohydrate replenishment in apple bark began as soon as the first leaves began to expand and was essentially complete by the time the new shoot had formed eight to ten leaves. Hansen (1971), also studying apple, reported that shoots became self-sufficient after the development of only five or six leaves. In the present study, carbohydrate levels in the 6-week and 3-week treatments in both gliricidia and

leucaena, were generally quite similar, although the 6-week treatment produced much more biomass during each growth interval. This would seem to indicate that, during the first six weeks of regrowth, photosynthate from new shoots was used to support growth rather than for replenishment of carbohydrate reserves.

The seasonally cut treatments were included in the present study, in part, to provide some indication of how quickly gliricidia and leucaena could replenish reserve carbohydrates that were used for regrowth after cutting. Trees in this treatment were cut at the end of the dry season and then allowed to grow undisturbed during the rainy season, a period of approximately seven months. Results were somewhat ambiguous due to high variability in the samples, and the effect of flower and fruit production in the leucaena plots. Nevertheless, some indication of replenishment rates was obtained. Table 31 shows starch and total reserve carbohydrate levels in the seasonally cut treatment, expressed as a percentage of carbohydrate values in the uncut control. As replenishment occurs, the difference between the two treatments should decrease, and percentages in the table should approach 100%.

Gliricidia was cut after the December 2 and March 5 sampling dates. In stems, starch concentrations in the seasonally cut treatment fell to 40% of the control after

Table 45. Starch and total reserve carbohydrates in the seasonally cut treatments of gliricidia and leucaena, expressed as a percentage of values in the uncut control treatments.

A. *Gliricidia sepium*

	Stem		Root	
Date	Starch (%)	Total (%)	Starch (%)	Total (%)
2 Dec 91	111	101	90	91
15 Jan 92	58	72	82	84
5 Mar 92	129	113	112	110
30 Apr 92	40	70	82	91
16 Jun 92	42	81	103	107
29 Jul 92	49	78	120	116
10 Sep 92	51	71	89	90
21 Oct 92	44	56	109	106

B. *Leucaena leucocephala*

	Stem		Root	
Date	Starch (%)	Total (%)	Starch (%)	Total (%)
22 Jan 92	65	86	88	95
11 Mar 92	34	77	74	99
4 May 92	16	45	32	59
19 Jun 92	53	65	50	74
3 Aug 92	49	57	85	93
15 Sep 92	42	84	49	83
27 Oct 92	203	136	64	72

the March cut, and then slowly increased to 51% by September 10. On October 21, starch concentrations decreased relative to the control, but this was due to a starch increase in the control, not to a decrease in the seasonally cut treatment. Starch replenishment in gliricidia stems began within three months of cutting, and levels were slightly higher on each succeeding date from June 16 to October 21. However, recovery was slow. At the end of seven months, starch in the seasonally cut treatment was still only about 50% of levels in the uncut control. Stem starch concentrations in the control increased considerably on the last sampling date, as reserves rose to high dry-season levels. Cutting may have delayed a similar increase in the seasonally cut treatment. If so, it occurred after sampling was completed. In gliricidia roots, two dry-season cuts had no definite effect on starch concentrations. Starch samples during the dry season were quite variable, so this may have obscured some treatment effects. Nevertheless, dry-season cutting seemed to have a minimal effect on carbohydrate levels in gliricidia. Erdmann (1991), in a study that included the end of the wet season and first half of the long dry season, also reported high variability in reserve carbohydrates in gliricidia.

Leucaena was cut after the January 22 and March 11 sampling dates. In contrast to gliricidia, dry-season cuts quickly affected reserve carbohydrate levels. In stems,

starch was significantly reduced after the first cut, and decreased further after the second cut. On May 4, starch concentrations in stems in the seasonally cut treatment were only 16% of those in the control. In roots, the first cut had no significant effect on starch concentrations in the seasonally cut treatment, but the second cut reduced starch to 32% of the control levels. From the low point in May, starch concentrations in both stems and roots steadily increased until the August sampling date. In August, root starch concentrations were at, and stem concentrations were close to, pre-cutting levels.

Leucaena trees in both the seasonally cut treatment and the control produced flowers and fruit during the wet season, but not at exactly the same time. The initiation of reproduction decreased the usefulness of "percentage of control concentrations" (Table 31) in evaluating the rate of carbohydrate replenishment because carbohydrate concentrations were affected by phenological stage. Roper et al. (1988) noted that carbohydrate accumulation may be interrupted by reproductive growth.

In the control, flower and fruit production began in late April and continued throughout the wet season. Starch in both stems and roots progressively decreased during this period and was lowest on October 21, the last sampling date. A slight increase in early August occurred at a time when no fruit was ripening. Trees in the seasonally cut treatment

flowered and produced fruit in August and September. This interrupted the accumulation of starch which had been observed prior to this time. Starch levels on September 15 were considerably lower than on August 3 (Table 20). After fruit had ripened, stem starch concentrations tripled in the seasonally cut treatment, and attained pre-cutting levels by October 21. In roots, starch in October remained at half the August level, but was similar to concentrations in the control trees. Guevarra et al. (1978) observed that leucaena cut at 18-week intervals had a longer lag phase during regrowth than did trees with shorter cutting intervals. They attributed this to a sink effect of flower and fruit production, which may have restricted starch accumulation. Results of the present study support this hypothesis.

Results indicate that sensitivity to cutting, and rate of carbohydrate replenishment vary according to species and plant part. Based on the starch-replenishment rate, leucaena seemed to recover substantially from cutting in as little as three months (May 4 - August 3), while stem starch in gliricidia was only 50% of the control after seven months. However, root starch in gliricidia was little affected by cutting so required no replenishment. To ensure complete replenishment of carbohydrate reserves, gliricidia might require a longer recovery period than leucaena.

It has been reported that if trees were cut at the proper time (early in the growing season), they could resprout, and still replenish starch reserves by the end of one growing season (Gregory & Wargo, 1986; Kays & Canham, 1991). Other studies have found that longer periods were required for complete replenishment of reserve carbohydrates after cutting. For two tropical savanna shrubs—*Clidemia sericea* and *Miconia albicans*—replenishment of root starch required one to two years (Miyanishi & Kellman, 1986). In *Betula pubescens*, one year was insufficient for complete recovery of root starch (Johansson, 1992). Starch in shoots of *Eucalyptus grandis* was equal to control levels nine months after cutting, but concentrations in *E. regnans* were lower (Old et al., 1990).

It must be noted that the gliricidia and leucaena trees in the seasonally cut treatment were not cut during the rainy season when growth was vigorous and reserve carbohydrate levels were low. Replenishment of reserves after a wet-season cut might require a longer period of time. Kays and Canham (1991) found that cutting at certain times during the summer resulted in low starch reserves at the end of the growing season and reduced sprout growth the following year.

The process of reserve carbohydrate replenishment might be hastened by increased photosynthesis in cut plants. Tschaplinski and Blake (1989) reported that shoot

decapitation in *Populus* resulted in reinvigoration of net photosynthesis in remaining foliage after four days, and accelerated net photosynthesis in subsequently produced coppice foliage. Net photosynthesis of coppice leaves was 23 times that of upper leaves on intact shoots 24 days after cutting. Increased net photosynthesis in remaining leaves after defoliation has also been reported by Wareing et al. (1968) and Satoh et al. (1977).

These results point to an area of research that has been neglected in agroforestry studies—the retention of some leaves or shoots in pruned trees. Tschaplinski and Blake (1994) found that starch decrease in *Populus* occurred only if defoliation exceeded 50%. Studies with tea have also shown that the retention of an uncut shoot reduced carbohydrate depletion and promoted replenishment (Nagarajah & Pethiyagoda, 1965; Kandiah, 1971; Kandiah et al., 1984).

<u>Effect of cutting on phenology and reserve carbohydrate cycles</u>

Cutting is known to affect the phenology of woody plants. Gliricidia, for example, is normally drought-deciduous, but after cutting will resprout and retain leaves during the dry season (Budowski, 1987; Catchpoole & Blair, 1990). This can affect the accumulation and use of reserve carbohydrates.

Both species in the present study produced and retained dry-season shoots and foliage after cutting. The main

effect of cutting in leucaena was an early reduction in starch and total reserve carbohydrate levels, which coincided with sprout growth (Figures 9-14). These dry-season reductions occurred while levels in the control treatment remained at a peak. Other than this, reserve carbohydrates in uncut and frequently cut leucaena trees followed basically the same trends, although levels of starch and total reserve carbohydrates were lower in the frequently cut trees (Figures 9-14). However, the sampling ended before dry-season carbohydrate accumulation had begun in the control trees. It is not known if frequently cut trees would have responded to the natural cycle of accumulation. Given their near-depletion levels of starch, they may have been unable to do so.

Another effect of altered phenology in leucaena was observed in the seasonally cut treatment, and was caused by delayed fruit production. Uncut leucaena trees had two main periods of fruit production during the wet season. The seasonally cut trees had only one period, which began later than in the control trees and ended sooner. When fruiting was completed in the seasonally cut treatment, stem starch concentrations rose to dry-season levels; concentrations in the still-fruiting control trees remained low.

Frequent cutting caused more deviation from normal reserve carbohydrate trends in gliricidia than in leucaena (Figures 2-7). In the control treatment of gliricidia, stem

and root sugar levels decreased during the wet season and remained fairly consistent until November, when they increased to dry-season highs. Starch levels were lowest during June and July, and then steadily increased. Total reserve carbohydrate cycles followed the trends of starch. In frequently cut trees, sugar did not decrease during the wet season. Rather, sugar levels increased in roots, and remained near the high dry-season levels in stems. Additionally, in contrast to the control trees, there was no accumulation of stem starch or total stem carbohydrates in frequently cut trees as the dry season approached. However, root starch increased on the last sample date, October 21 (Tables 6 and 7). Evidently, the natural cycle of accumulation, although delayed, was still intact after repeated cutting during the preceding eleven months. The source of the additional root starch is not known. Biomass production during the preceding growth interval had not declined, nor had sugar levels decreased. Perhaps cessation of below-ground growth provided the carbohydrate supply. In temperate zone trees, use of carbohydrates for root elongation generally begins earlier in the season than for shoot elongation, and continues for several weeks after shoot growth ceases. In recurrently flushing species, however, the use of carbohydrates for root growth may continue for only a short time after shoot elongation stops (Kozlowski, 1971). This pattern might also apply in

gliricidia, which sheds leaves and ceases shoot growth during the dry season. Perhaps the approach of the dry season triggered an end to root growth and freed carbohydrates for storage. Even when cut trees continue shoot growth during the dry season, growth is greatly reduced, and this might be adequate to prompt the cessation of root growth. In a seasonally dry region in India, nonstructural carbohydrates in the fine roots of teak (*Tectona grandis*) were highest during the dry season and at a minimum in the early part of the rainy season when active root growth resumed. Once carbohydrate stores in fine roots were at minimal levels, additional growth depended on carbohydrates from current photosynthesis or stores in the large roots (Singh & Srivastava, 1986).

Total reserve carbohydrates in roots of frequently cut gliricidia trees, as with starch, increased as the dry season approached, but accumulation occurred later than in control trees (Tables 6 and 7). On October 21, all four gliricidia treatments had very similar total reserve carbohydrate concentrations in the roots, although the proportions of sugar and starch were quite different among treatments (Tables 4-7).

Dry Matter Production

It has been reported that frequent cutting will decrease biomass production in agroforestry trees (Guevarra et al., 1978; Osman, 1981; Duguma et al., 1988; Ella et al.,

1989). This was also found to be true in the present study (Tables 10, 11, 25, 26). Cumulative dry matter production in gliricidia during the study period was 10.6 kg tree^{-1} in the seasonally cut treatment, 1.7 kg tree^{-1} in the 6-week treatment, and 0.8 kg tree^{-1} in the 3-week treatment. Respective figures for leucaena were 5.7 kg tree^{-1}, 1.2 kg tree^{-1}, and 0.5 kg tree^{-1}. Assuming 5000 trees per hectare, estimated annual dry matter production in this experiment would be, for gliricidia and leucaena respectively: seasonally cut treatment, 53.0 Mg ha^{-1} year^{-1} and 28.5 Mg ha^{-1} year^{-1}; 6-week treatment, 8.5 Mg ha^{-1} year^{-1} and 6.0 Mg ha^{-1} year^{-1}; 3-week treatment, 4.0 Mg ha^{-1} year^{-1} and 2.5 Mg ha^{-1} year^{-1}.

Biomass production, as reported for agroforestry trees, is affected by climate, soil fertility, cutting frequency, management system, plant age, stand density, genetic variety, and plant part under consideration (e.g., woody parts or parts suitable for fodder). This makes comparisons difficult. In gliricidia, reported values for annual leaf dry-matter production generally range from 2 to 20 Mg year^{-1} (Simons & Stewart, 1994). The range of dry matter values for leucaena edible fodder yields is 3 to 30 Mg ha^{-1} year^{-1} (Shelton & Brewbaker, 1994), 5.3 to 33.1 Mg ha^{-1} year^{-1} (Pound & Martinez Cairo, 1983), or 6 to 18 Mg ha^{-1} year^{-1} (NAS, 1984). Pound and Martinez Cairo (1983) state that the

expected range for farm yields of edible leucaena fodder is 5 to 15 Mg ha^{-1} year^{-1}.

In alley cropping research at IITA, the following dry matter yields have been reported: 5.18 Mg ha^{-1} year^{-1} in gliricidia and 8.64 Mg ha^{-1} year^{-1} in leucaena cut five times per year (IITA, 1983); 5.5 Mg ha^{-1} year^{-1} in gliricidia and 7.4 Mg ha^{-1} year^{-1} in leucaena cut five times (Juo & Kang, 1989); 5 to 8 Mg ha^{-1} year^{-1} for leucaena cut five or six times (Kang et al., 1981, 1985); 3.11 Mg ha^{-1} from three growing-season cuts in September to November, and 6.98 Mg ha^{-1} from three cuts in April to July (Palada et al., 1992); and almost 6 Mg ha^{-1} year^{-1} for young gliricidia cut two or three times (Atta-Krah and Sumberg, 1988).

In comparison with other studies conducted at IITA, dry matter estimates in the present study might seem high, especially considering the number of cuts in the 3-week and 6-week treatments. This is probably due to plot management during the study. Weeds in alleys were manually cut or killed with herbicides as needed, thereby providing mulch and minimizing competition for resources. The alley cropping configuration, with its low density, also reduced competition between trees. As a result, conditions were favorable for the rapid growth of individual trees. The cutting regime in the seasonally cut treatment also favored rapid growth; these trees were left uncut for seven months during the rainy season, when most growth occurs. During

this period, the amount of biomass produced by gliricidia trees in the seasonally cut treatment was 65% of the dry matter in control trees which had not been cut in two years. In leucaena, the percentage was 75%. Growth rates would be expected to decrease after canopy closure. Considering the favorable conditions, the observed dry matter values are reasonable.

Biomass production in the 6-week cutting treatments was significantly higher than in the 3-week treatments (sum of 2 cuts) despite similar reserve carbohydrate levels (Tables 11, 26). The amount of time spent in the linear growth phase accounts for this difference. Erdmann (1991) estimated that gliricidia sprouts enter the linear growth phase approximately three weeks after cutting. Guevarra et al. (1978) reported a 3- to 4-week lag phase in leucaena regrowth after cutting. Based on these reports, the 3-week treatments had just entered the rapid linear growth phase when they were re-cut. The 6-week treatment continued in this phase for an additional 3 weeks, resulting in higher dry matter production. These results illustrate that too-frequent cutting, regardless of its impact on reserve carbohydrate levels, can reduce biomass production.

Interestingly, at the last cut (December 1992), when both treatments had been allowed to grow for 6 weeks, the 3-week treatment actually produced significantly more biomass than the 6-week treatment. Perhaps the 3-week

cutting regime had acclimated these plants to respond quickly after cutting, or perhaps they contained higher levels of growth regulators which enhanced sprouting ability. Taylor et al. (1982) reported a large increase in root-produced cytokinins ten days after decapitation in *Eucalyptus camaldulensis*, and observed that enhanced shoot growth was correlated with higher cytokinin concentrations and a mobilization of gibberellins in the stump. Satoh et al. (1977) reported increased activity in cytokinin-like substances 13 days after decapitation of *Morus alba*. Mika (1986) found that during the time of rapid bud development, cytokinin levels in pruned apple trees were four times higher than in unpruned trees.

Post-cutting biomass production increased dramatically with the onset of the rainy season. For example, in the 6-week cutting treatment, gliricidia biomass production increased more than five times from the March 5 cutting date to the April 30 cutting date (the first wet-season growth interval) (Table 12). In leucaena, biomass production more than doubled in the 6-week treatment during this period, and during the next growth interval, it was three times higher than production during the dry season (Table 27). Even the 3-week treatments, which were cut twice as often during the wet season as during the dry season, experienced a 1.5- to two-times increase in biomass production when the rains began (Tables 13, 28). These findings are in accord with

phenological studies of tree growth in seasonally dry regions (Huxley & Van Eck, 1974; Alvim & Alvim, 1978; Bullock & Solis-Magallanes, 1990; Wright, 1991; Borchert, 1994). Ella et al. (1989) reported that gliricidia and leucaena yields were positively correlated to rainfall in the seasonally dry tropics. Budelman (1987) also reported such a correlation for gliricidia. Duguma et al. (1988) found that two-thirds of the annual biomass production of leucaena occurred during the six-month rainy season.

Catchpoole & Blair (1990) reported that dry-season leaf production in gliricidia was lower than that in leucaena, but wet-season production was greater. In the present study, dry-season production in the two species seemed to be similar (Tables 10 and 25). Wet-season production in all three cutting treatments was greater in gliricidia than in leucaena. In the 6-week and 3-week treatments, the difference between gliricidia and leucaena was the result of high production by gliricidia during the first wet-season growth interval—May, 1992 (Tables 11, 26). Otherwise, production in gliricidia and leucaena in these two treatments was quite similar.

The ability of gliricidia to respond more quickly to increased rainfall might be related to gliricidia's relatively high level of stem starch (in comparison to leucaena). During the first wet-season growth interval, stem starch in the frequently cut treatments of both species

was decreased by 60-70 percent (Tables 6, 7, 21, 22). This amounted to a reduction of about 25 mg g^{-1} in gliricidia, but only 6-9 mg g^{-1} in leucaena. The proximity of large starch reserves to expanding buds might have supported rapid growth in gliricidia once conditions became favorable.

The difference between the two species with regard to biomass production was decreased by frequent cutting. In the seasonally cut treatment, gliricidia produced 1.8 times more biomass than leucaena; in the 6-week treatment, gliricidia produced 1.4 times more; and in the 3-week treatment, gliricidia produced 1.2 times more.

Several authors have reported that as cutting intervals increase, woody stems comprise a larger proportion of a tree's dry matter production (Guevarra et al., 1978; Duguma et al., 1988; Ella et al., 1989; Stür et al., 1994). In contrast, Osman (1981) found that leaf to stem ratios did not change in leucaena cuttings ranging in age from 30 to 150 days. Results of the present study indicate that proportions of leaves and stems do change as cutting intervals are lengthened. In gliricidia, with cutting intervals of 3 weeks, 6 weeks, 32 weeks, and 23 months, leaf percentage of above-ground biomass was 69%, 61%, 20%, and 9% respectively. In leucaena, corresponding leaf percentages were 72%, 57%, 17%, and 12%. In the 3-week and 6-week cutting intervals, stems were green and succulent; in the longer cutting intervals wood composed a large part of the

stem biomass. These results illustrate the importance of adjusting the length of cutting intervals in order to maximize production of the desired output, for example, edible fodder versus fuelwood.

Relationship between reserve carbohydrates and dry matter production

It is difficult to prove a direct causal effect between reserve carbohydrate levels and shoot growth. Nonetheless, a number of studies have correlated low carbohydrate concentrations with low sprout production. Positive correlations between reserve carbohydrate levels and degree of sprouting in pruned or coppiced woody species have been reported for chamise (*Adenostoma fasciculatum*) (Jones & Laude, 1960; Laude et al., 1961); aspen (*Populus tremuloides*) (Tew, 1970; Schier & Zasada, 1973); Colorado range species (Menke & Trlica, 1981); desert shrubs (Trlica & Cook, 1971); mesquite (*Prosopis glandulosa*) (Wright & Stinson, 1970); four temperate hardwood species (Kays & Canham, 1991); heather (*Calluna vulgaris*) (Berdowski & Seipel, 1988), and two tropical savanna shrubs (Miyanishi & Kellman, 1986). In contrast, Nagarajah and Pethiyagoda (1965) found no direct relationship between root reserve carbohydrates and bud growth in tea. Wenger (1953) reported similar findings for sweetgum (*Liquidamber styraciflua*), and speculated that hormones were the factor responsible for seasonal trends in sprout production.

In the present study, significant correlations were found between reserve carbohydrate levels and dry matter production in the 3-week and 6-week treatments during the wet season, and in all three cutting treatments for the period of October to December, 1992 (Tables 14, 15, 29, 30). All correlations were based on plot- or sampling-date means, not on samples from individual trees. Nevertheless, results support the hypothesis that initial carbohydrate levels will affect subsequent sprout production.

It was found that carbohydrate values from the beginning of a growth interval were more strongly correlated to biomass production than were carbohydrate values from the end of the growth interval. Unfortunately, this reduced the value of my samples for correlation analysis. My carbohydrate and biomass samples, although collected from the same trees, were also from the same date, at the end of the growth interval.

While data collected in this study indicate a general relationship between initial reserve carbohydrate levels and biomass production, it must be cautioned that yield predictions based on measurements in individual trees may be unreliable. Factors such as species, climate, microclimate, and genotype will complicate predictions. Also, our understanding of coppice physiology is incomplete. Sennerby-Forsse et al. (1992, p. 167) state, "In coppice, the high complexity of interacting physiological processes

such as dynamics and interactions of growth regulators, water, nutrients and storage products makes it difficult to isolate single factors responsible for certain responses."

CHAPTER 4
RESERVE CARBOHYDRATE CYCLES IN THE LOWER BOLES AND STRUCTURAL ROOTS OF FIVE UNCUT MULTIPURPOSE TREE SPECIES

Materials and Methods

Study Site

The study was conducted at the main research station of the International Institute of Tropical Agriculture (IITA) in Ibadan, Nigeria (latitude 7° 30' N and longitude 3° 54' E). A site description of the study area is given at the beginning of Chapter 3. Field work for the present study was conducted at the IITA arboretum from November, 1991 to November, 1992. The soil of this site was classified as an Oxic Paleustalf, and texturally as a sandy clay loam.

The arboretum was established in June, 1979 as part of an IITA/International Development Research Centre (IDRC) agroforestry project. Selected tropical multipurpose tree species were planted in 10m X 20m blocks, with one species in each block. Tree spacing within blocks was 2m X 4m. Management precluded cutting or pruning of arboretum trees.

Five species were selected for inclusion in this study: *Dactyladenia barteri*, *Gliricidia sepium*, *Leucaena*

leucocephala, *Pterocarpus soyauxii*, and *Senna siamea* (Table 32). They include two indigenous and three exotic species, and three nitrogen-fixers and two non-nitrogen-fixers. The five species also have a wide range of seasonal growth patterns, as described in the "Multipurpose Trees" section of Chapter 2.

Table 32. Characteristics of five species of multipurpose trees that were included in the IITA arboretum study.

Species	Native Region	Trunk Diameter[1] (cm)	Height[1] (m)	N-fixer
Gliricidia sepium	C. America	25	12	Yes
Leucaena leucocephala	C. America	42	19	Yes
Senna (Cassia) siamea	S.E. Asia	37	16	No
Dactyladenia (Acioa) barteri	W. Africa	29	7.5	No
Pterocarpus soyauxii	W. Africa	42	17	Yes

[1]Trunk diameter and height are mean values for the four trees per species included in this study. Trunk diameter was measured at 25 cm above ground level.

Experimental Design and Sampling Procedure

Four trees of each species were randomly selected from among the dominant and codominant trees in the arboretum's planting blocks. Suppressed trees were excluded in order to minimize the effects of stress and competition. The same

four individuals of each species were sampled approximately monthly during one year. According to Priestley (1962), it should be possible to detect seasonal changes in trees by using small numbers of trees (or even single trees) provided that small representative samples can be taken from the same tree(s) without fundamentally altering the course of their metabolism.

On each sample date, an increment borer (4.3 mm diameter) was used to remove two 3-cm-long wood cores from tree boles, approximately 25 cm above the ground. Two wood cores were taken from large lateral roots only on every third sample date (4 times total) to avoid possible tree damage. Wood cores, from which the bark was removed, were immediately placed in vials in an ice-filled cooler and transported to the lab. The cores were frozen at 0°C, and then freeze-dried as soon after collection as possible. Freeze-dried samples were ground to pass through a 40-mesh screen.

Monthly observations were recorded on each tree's phenological stage, including active shoot growth, leaf senescence and fall, leaf flush, flowering, and fruiting. Daily values for rainfall (mm), solar radiation (W m^{-2}), minimum and maximum temperatures (°C), and minimum and maximum relative humidity (%) were obtained from IITA's automated weather station. These values were used to

calculate means for each weather variable, during each sample interval (the period between two sampling dates).

Carbohydrate Analysis

Chemical analysis of ground wood samples followed the procedure described in Chapter 3.

Statistical Analysis

The seasonal study of reserve carbohydrates in arboretum trees was conducted in a split-plot (repeated measures) design with four replicates of each tree species. Species comprised the main plot, and sampling date the sub-plot. GLM procedure of the Statistical Analysis System was used to analyze data (SAS Institute, 1988). Means were compared using Duncan's multiple range test at the 5% level.

Associations between reserve carbohydrate variables and weather variables were evaluated using linear regression and correlation analysis. In addition, principal components analysis (Johnson and Wichern, 1988) was used to calculate weather covariates that summarized the information contained in the individual weather variables, given the correlations between them. To identify differing responses among species, monthly reserve carbohydrate concentrations in each species were regressed on weather covariates, and slopes were compared for significant differences at the 5% level (i.e., tested for homogeneity of regression coefficients).

Experimental Results

Mean Annual Reserve Carbohydrate Concentrations

Analysis of variance revealed significant differences among species with regard to mean annual reserve carbohydrate concentrations in both boles and roots (Table 33). Since the roots were sampled only four times, at intervals of three months, root means should be considered as only rough estimates.

In general terms, *D. barteri* had the lowest mean annual concentrations of reserve carbohydrates in the bole, gliricidia had intermediate levels, and the other three species had higher levels. Mean sugar concentrations ranged from 22.4 mg g^{-1} to 40.1 mg g^{-1}, starch concentrations from 5.2 mg g^{-1} to 22.6 mg g^{-1}, and total reserve carbohydrates from 27.6 mg g^{-1} to 57.9 mg g^{-1}. *D. barteri* had significantly lower concentrations of sugar, starch, and total reserve carbohydrates in boles than the other species. *G. sepium* was significantly higher than *D. barteri*, but significantly lower than the other species for all three carbohydrate variables. For sugar, *S. siamea* was significantly higher than *P. soyauxii*, which was significantly higher than *L. leucocephala*. For starch, leucaena was significantly higher than the other species. Despite differences in sugar and starch, total reserve carbohydrate concentrations in

Table 33. Mean annual reserve carbohydrate concentrations in five multipurpose tree species

A. LOWER BOLES

Tree Species[1]	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Db	22.4 e	5.2 d	27.6 c	81.1 a
Gs	25.9 d	8.1 c	33.9 b	76.4 b
Ll	32.1 c	22.6 a	54.7 a	57.9 e
Ps	37.5 b	17.7 b	55.2 a	66.6 d
Ss	40.1 a	17.8 b	57.9 a	69.6 c

B. STRUCTURAL ROOTS

Tree Species	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Db	24.3 b	9.0 c	33.2 c	73.6 a
Gs	27.9 b	15.8 b	43.7 b	66.3 b
Ll	26.9 b	18.9 ab	45.8 b	57.7 c
Ps	41.5 a	23.4 a	64.9 a	63.8 b
Ss	40.9 a	16.6 b	57.5 a	70.8 a

[1] Db = *Dactyladenia barteri*; Gs = *Gliricidia sepium*; Ll = *Leucaena leucocephala*; Ps = *Pterocarpus soyauxii*; Ss = *Senna siamea*

[2] Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Each mean is based on 4 trees which were sampled from November, 1991 through October, 1992. Stem means are based on 10 sample dates (n=40). Root means are based on 4 sample dates (n=16).

leucaena, *S. siamea*, and *P. soyauxii* were very similar and not significantly different.

Species rankings and carbohydrate concentrations in roots appear similar to those in boles. Based on root carbohydrate concentrations, however, leucaena would move into the intermediate category, along with gliricidia.

Annual Trends in Reserve Carbohydrate Concentrations

Definite trends in reserve carbohydrates were observed during the one-year study period (Figure 16; Table 34). Combining the values from all five species revealed the following trends for reserve carbohydrates in lower boles.

(1) Sugar concentrations were highest during the second half of the long dry season (January - March), and lowest during the second half of the rainy season and the beginning of the long dry season (July - November).

(2) Starch concentrations were highest at the beginning of the rainy season (April - May), but were not significantly lower during the dry-season months of November and December. There was a decrease in starch during January and March that coincided with the peak sugar values. The lowest starch concentrations were noted from June through early October, after which they began to rise.

(3) Total reserve carbohydrate concentrations were highest during the dry season and the beginning of the rainy season (December - April). During this period, total reserve

carbohydrate values were very consistent from month to month. The lowest total reserve carbohydrate concentrations occurred during the second half of the rainy season (July - October). In all cases, comparisons of high and low carbohydrate values revealed significant differences.

Reserve carbohydrate trends in structural roots apparently followed that described for lower boles, but this cannot be said with certainty because of the low number of sample dates. For example, no samples were taken during April and May when starch in boles was highest. Given this limitation, high and low values in roots seemed to coincide with those in boles. Additional support for this position was provided by the trends observed for gliricidia and leucaena in the control treatments of the cutting frequency study (Chapter 3).

Tables 35-39 and Figures 17-21 show the reserve carbohydrate trends in the five different species. Each species conforms to the general trends outlined above, but there are differences. High and low values sometimes occur earlier or later, and persist for longer or shorter periods, in different species. Sugar and total reserve carbohydrate trends were especially consistent among species: concentrations were highest during the dry season and lowest during the rainy season. Starch followed the same trend but there was more variability in the timing of high values during the dry season. In *D. barteri* and *G. sepium*, starch

Table 34. All species combined: Reserve carbohydrate concentrations from November 1991 to November 1992.

A. LOWER BOLES

Sample Date	Sugar[1] ($mg\ g^{-1}$)	Starch ($mg\ g^{-1}$)	Total ($mg\ g^{-1}$)	Sugar %
14 Nov 91	22.9 de	15.1 bcd	37.9 cd	62.1 f
20 Dec 91	39.5 b	16.7 ab	56.2 a	71.3 bcd
24 Jan 92	46.3 a	13.4 cde	59.8 a	78.4 a
17 Mar 92	43.2 a	15.7 bc	58.9 a	75.2 ab
21 Apr 92	37.4 b	19.4 a	56.7 a	68.4 de
22 May 92	32.3 c	17.5 ab	49.8 b	68.5 de
24 Jun 92	26.3 d	12.0 def	38.3 cd	70.4 cde
27 Jul 92	24.3 de	9.5 f	33.8 cd	74.3 bc
28 Aug 92	22.9 de	11.3 ef	34.2 cd	68.3 de
5 Oct 92	20.7 e	12.2 def	32.9 d	66.3 e
11 Nov 92	22.6 de	16.5 abc	39.1 c	60.8 f

B. STRUCTURAL ROOTS

Sample Date	Sugar ($mg\ g^{-1}$)	Starch ($mg\ g^{-1}$)	Total ($mg\ g^{-1}$)	Sugar %
14 Nov 91	26.6 b	21.5 a	48.1 b	55.0 c
17 Mar 92	45.2 a	17.7 b	62.9 a	72.8 a
24 Jun 92	29.9 b	16.7 b	46.6 b	65.7 b
5 Oct 92	27.5 b	11.1 c	38.6 c	72.3 a

[1] Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees of each species (n=20), which were sampled repeatedly over the course of the experiment.

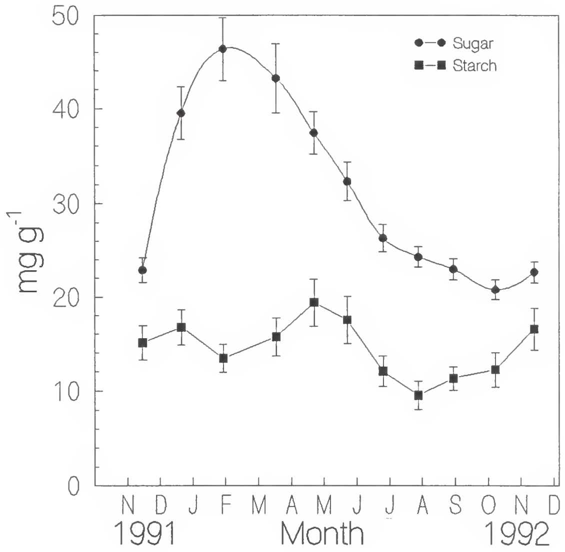

Figure 16. Stem carbohydrates in the arboretum trees, all species combined. Each point is the mean (± S.E.) of 20 observations.

Table 35. *Dactyladenia barteri*: Reserve carbohydrate concentrations (mg g^{-1}) from November 1991 to November 1992.

A. LOWER BOLES

Sample Date	Sugar[1]	Starch	Total	Sugar %
14 Nov 91	17.3 de	6.6 a	23.9 bcd	72.0 b
20 Dec 91	22.9 cd	7.0 a	29.8 ab	76.9 ab
24 Jan 92	29.0 ab	6.7 a	35.7 a	81.5 ab
17 Mar 92	24.3 bc	5.0 a	29.4 ab	83.2 a
21 Apr 92	31.5 a	5.7 a	37.2 a	84.6 a
22 May 92	25.0 bc	5.5 a	30.5 ab	82.8 a
24 Jun 92	21.3 cde	5.4 a	26.7 bc	80.4 ab
27 Jul 92	20.2 cde	3.1 a	23.4 bcd	86.9 a
28 Aug 92	16.7 de	4.5 a	21.2 cd	80.4 ab
5 Oct 92	15.6 e	2.7 a	18.3 d	84.6 a
11 Nov 92	16.3 e	6.5 a	22.8 bcd	72.3 b

B. STRUCTURAL ROOTS

Sample Date	Sugar	Starch	Total	Sugar %
14 Nov 91	24.0 a	14.5 a	38.5 a	61.5 b
17 Mar 92	26.3 a	6.1 b	32.4 a	81.2 a
24 Jun 92	23.5 a	7.5 b	31.0 a	76.8 a
5 Oct 92	23.2 a	7.9 b	31.1 a	75.1 a

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees sampled repeatedly over the course of the experiment.

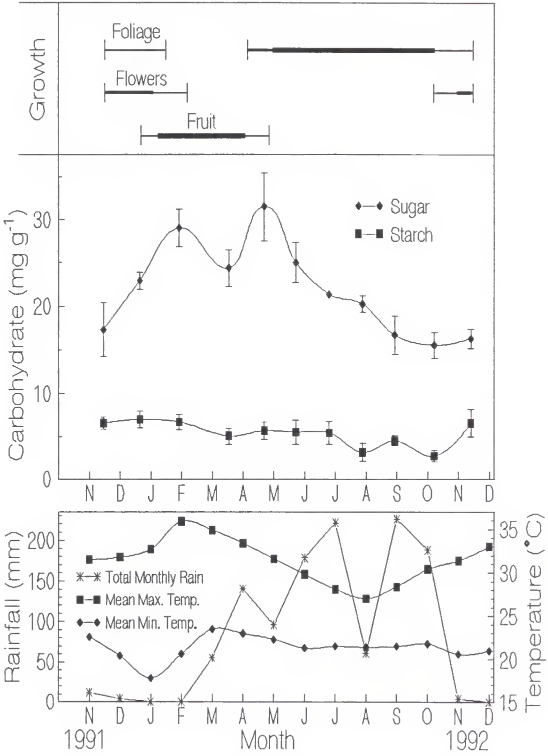

Figure 17. *Dactyladenia barteri*: Stem carbohydrates and phenology. Carbohydrate means (± S.E.) are based on four observations. Thickness of growth lines indicates relative amount of growth.

Table 36. *Gliricidia sepium*: Reserve carbohydrate concentrations ($mg\ g^{-1}$) from November 1991 to November 1992.

A. LOWER BOLES

Sample Date	Sugar[1]	Starch	Total CHO	Sugar %
14 Nov 91	18.7 d	12.8 ab	31.5 b	60.2 d
20 Dec 91	30.3 ab	11.8 ab	42.2 a	71.6 c
24 Jan 92	34.6 a	8.2 bcd	42.8 a	81.5 ab
17 Mar 92	26.6 bc	7.3 bcd	33.9 ab	78.3 abc
21 Apr 92	27.0 bc	9.8 abc	36.7 ab	73.6 bc
22 May 92	25.6 bcd	5.5 cd	31.1 b	82.2 ab
24 Jun 92	27.4 bc	5.0 cd	32.4 b	83.9 a
27 Jul 92	24.2 bcd	3.4 d	27.6 b	86.8 a
28 Aug 92	23.7 bcd	8.2 bcd	31.9 b	74.2 bc
5 Oct 92	20.6 cd	8.5 bcd	29.1 b	71.4 c
11 Nov 92	20.4 cd	14.5 a	34.9 ab	60.2 d

B. STRUCTURAL ROOTS

Sample Date	Sugar	Starch	Total CHO	Sugar %
14 Nov 91	25.0 b	25.7 a	50.7 ab	49.1 c
17 Mar 92	36.8 a	20.0 ab	56.8 a	65.3 b
24 Jun 92	25.8 b	12.8 bc	38.6 bc	66.9 b
5 Oct 92	24.0 b	4.7 c	28.7 c	83.9 a

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees sampled repeatedly over the course of the experiment.

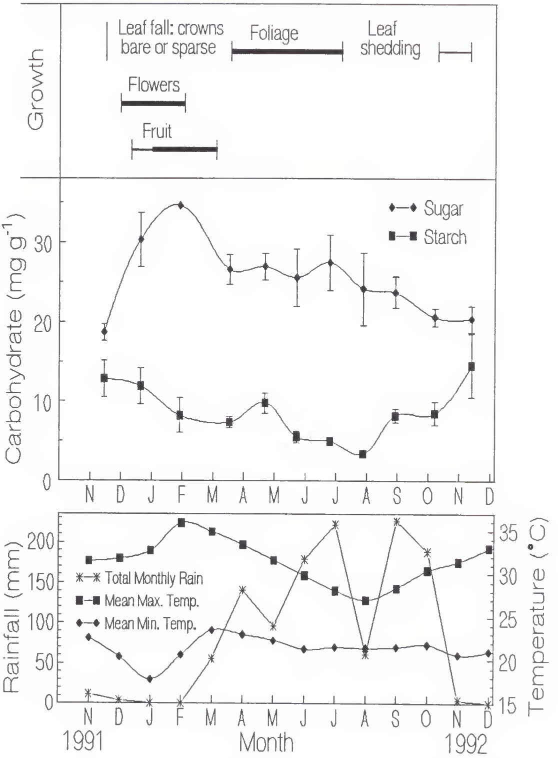

Figure 18. *Gliricidia sepium*: Stem carbohydrates and phenology. Carbohydrate means (± S.E.) are based on four observations. Thickness of growth lines indicates relative amount of growth.

Table 37. *Leucaena leucocephala*: Reserve carbohydrate concentrations (mg g^{-1}) from November 1991 to November 1992.

A. LOWER BOLES

Sample Date	Sugar[1]	Starch	Total	Sugar %
14 Nov 91	20.9 d	24.9 abc	45.8 bc	48.0 d
20 Dec 91	45.4 ab	24.9 abc	70.3 a	64.6 abc
24 Jan 92	49.4 a	15.7 bc	65.1 a	76.1 a
17 Mar 92	48.7 a	21.8 abc	70.5 a	68.9 ab
21 Apr 92	39.5 bc	32.2 a	71.7 a	54.9 cd
22 May 92	32.3 c	32.7 a	64.9 a	49.3 d
24 Jun 92	20.1 d	14.1 c	34.2 c	59.3 bcd
27 Jul 92	23.8 d	19.7 bc	43.5 bc	55.0 cd
28 Aug 92	20.6 d	17.9 bc	38.5 bc	53.7 cd
5 Oct 92	20.4 d	22.2 abc	42.5 bc	49.3 d
11 Nov 92	24.4 d	26.3 ab	50.7 b	49.4 d

B. STRUCTURAL ROOTS

Sample Date	Sugar	Starch	Total	Sugar %
14 Nov 91	17.0 b	19.7 n.s.	36.7 b	46.0 c
17 Mar 92	43.8 a	20.1 n.s.	63.9 a	69.0 a
24 Jun 92	24.3 b	22.5 n.s.	46.8 b	52.1 bc
5 Oct 92	22.4 b	13.2 n.s.	35.6 b	63.8 ab

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees sampled repeatedly over the course of the experiment.

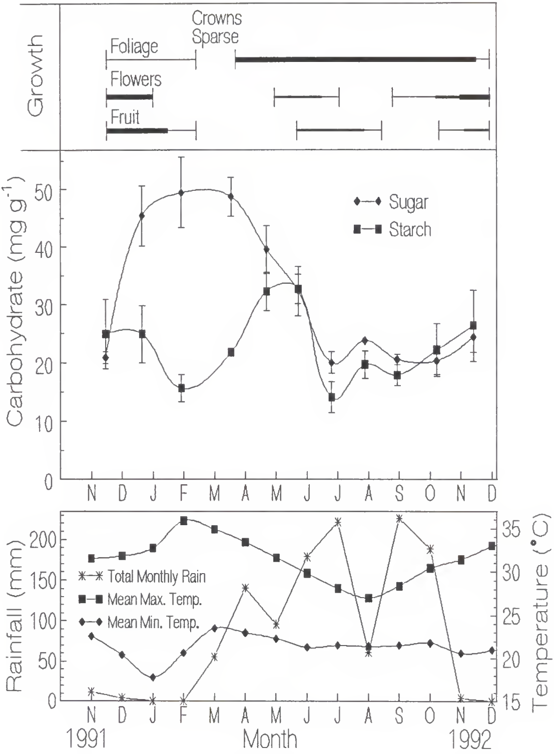

Figure 19. *Leucaena leucocephala*: Stem carbohydrates and phenology. Carbohydrate means (± S.E.) are based on four observations. Thickness of growth lines indicates relative amount of growth.

Table 38. *Pterocarpus soyauxii*: Reserve carbohydrate concentrations (mg g^{-1}) from 14 November 1991 to 11 November 1992.

A. LOWER BOLES

Sample Date	Sugar[1]	Starch	Total CHO	Sugar %
14 Nov 91	29.4 e	18.6 abc	47.9 de	61.3 ef
20 Dec 91	50.4 ab	16.5 c	66.9 ab	75.5 a
24 Jan 92	55.7 a	17.2 bc	72.9 a	76.3 a
17 Mar 92	53.4 a	20.3 abc	73.7 a	72.7 ab
21 Apr 92	43.9 bc	19.1 abc	63.0 abc	69.1 bcd
22 May 92	38.8 cd	20.8 abc	59.6 bcd	65.0 cde
24 Jun 92	31.6 de	22.5 ab	54.1 cd	58.1 fg
27 Jul 92	25.8 ef	10.7 d	36.5 e	70.6 abc
28 Aug 92	26.4 ef	15.1 cd	41.5 e	63.4 def
5 Oct 92	19.3 f	16.4 c	35.7 e	54.3 gh
11 Nov 92	24.4 ef	23.3 a	47.6 de	51.8 h

B. STRUCTURAL ROOTS

Sample Date	Sugar	Starch	Total CHO	Sugar %
14 Nov 91	39.3 b	27.9 a	67.1 b	59.5 b
17 Mar 92	60.1 a	20.7 a	80.8 a	74.6 a
24 Jun 92	37.4 b	28.7 a	66.1 b	56.6 b
5 Oct 92	29.2 c	16.4 a	45.6 c	64.6 b

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees sampled repeatedly over the course of the experiment.

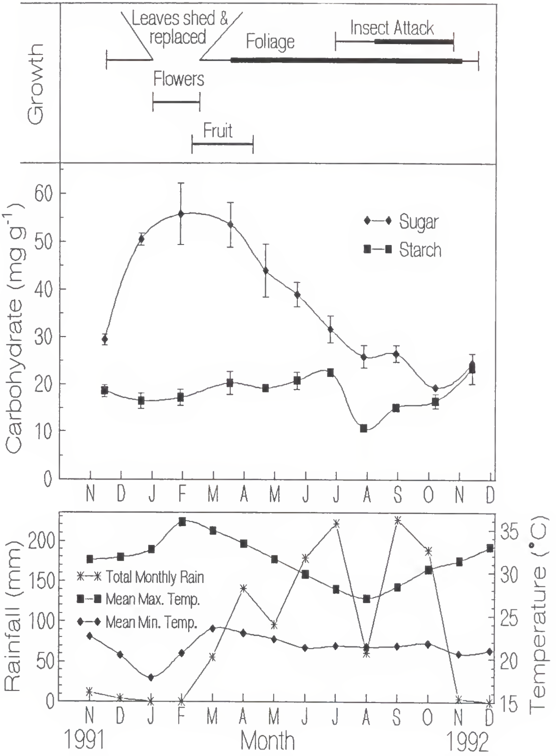

Figure 20. *Pterocarpus soyauxii*: Stem carbohydrates and phenology. Carbohydrate means (± S.E.) are based on four observations. Thickness of growth lines indicates relative amount of growth.

Table 39. *Senna siamea*: Reserve carbohydrate concentrations ($mg\ g^{-1}$) from November 1991 to November 1992.

A. LOWER BOLES

Sample Date	Sugar[1]	Starch	Total CHO	Sugar %
14 Nov 91	28.0 d	12.5 cd	40.5 d	69.2 abc
20 Dec 91	48.6 b	23.3 ab	71.9 bc	67.6 bcd
24 Jan 92	62.9 a	19.4 bc	82.3 ab	76.8 a
17 Mar 92	62.9 a	24.1 ab	87.0 a	72.9 ab
21 Apr 92	45.0 bc	30.0 a	75.1 b	60.0 d
22 May 92	39.8 c	23.1 ab	62.9 c	63.2 cd
24 Jun 92	31.0 d	13.2 cd	44.2 d	70.4 abc
27 Jul 92	27.3 d	10.7 d	38.0 d	72.0 ab
28 Aug 92	27.4 d	10.6 d	38.0 d	72.5 ab
5 Oct 92	27.8 d	11.3 d	39.1 d	71.9 ab
11 Nov 92	27.7 d	11.7 d	39.4 d	70.2 abc

B. STRUCTURAL ROOTS

Sample Date	Sugar	Starch	Total CHO	Sugar %
14 Nov 91	27.6 b	19.6 a	47.2 b	58.8 b
17 Mar 92	59.2 a	21.4 a	80.5 a	74.0 a
24 Jun 92	38.3 b	12.2 a	50.5 b	76.2 a
5 Oct 92	38.7 b	13.3 a	52.0 b	74.3 a

[1]Means were compared using Duncan's multiple range test at the 5% level. Means in the same column that are followed by the same letter are not significantly different. Means are based on 4 trees sampled repeatedly over the course of the experiment.

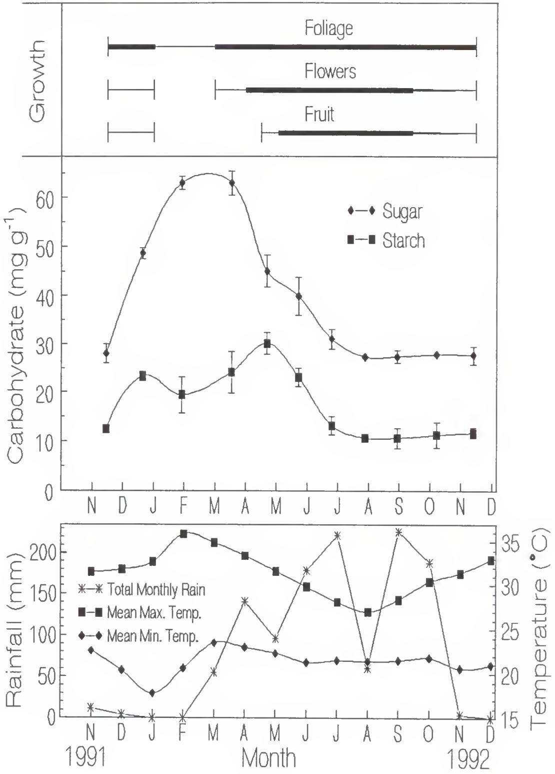

Figure 21. *Senna siamea*: stem carbohydrates and phenology. Carbohydrate means (± S.E.) are based on four observations. Thickness of growth lines indicates relative amount of growth.

peaked earlier (November and December) than in the other species. Additionally, each species—except *D. barteri*—experienced a one- or two-month decrease in starch at some time between December and March. The exact timing of this decrease varied.

For all species, there were significant differences between lowest and highest reserve carbohydrate values in the lower boles (except for starch in *D. barteri*).

Effect of Weather on Reserve Carbohydrate Concentrations

Significant correlations were found between reserve carbohydrate concentrations and a number of weather variables (Tables 40-45). Weather variables included in this analysis were rainfall (mm), solar radiation (W m^{-2}), minimum and maximum temperature (°C), minimum and maximum relative humidity (%), and weather covariate—a value, calculated by principal components analysis, that summarized the weather variables, given the correlations between them. All weather variables were means for sampling intervals (the period from one sampling date to the next sampling date).

The strongest correlations were between the weather variables and sugar concentrations. When carbohydrate values for the five tree species were evaluated together, all correlations between weather variables and sugar were significant (Table 40). In boles, sugar was most highly correlated with minimum relative humidity and maximum

temperature. The weakest correlation was between bole sugar and minimum temperature. In roots—based on only four dates—the strongest correlations were between sugar and the temperature and relative humidity variables.

Starch concentrations were not as strongly correlated to weather variables as were sugar concentrations. In boles, starch was significantly correlated with solar radiation, minimum and maximum temperatures, and minimum relative humidity. The highest correlation coefficient was 0.23, for maximum temperature. In roots, only rainfall was significantly correlated with starch ($r = 0.29$). The lower number of significant correlations for root starch is at least partially attributable to fewer degrees of freedom in the root analyses; correlation coefficients for roots were often similar to those calculated for boles.

Correlations between weather variables and total reserve carbohydrates were very similar to those between the weather variables and sugar, but correlation coefficients were somewhat lower for total reserve carbohydrates. Additionally, minimum temperature was not significantly correlated with total reserve carbohydrates.

Tables 41-45 show the correlation coefficients for each species. It is apparent that differences exist among species concerning the response of reserve carbohydrates to different weather variables. These differences are most obvious for starch.

Table 40. All species combined: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficient (r)			
	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.57 ***	-0.19 **	-0.48 ***	-0.19 **
Rain	-0.49 ***	-0.10	-0.39 ***	-0.16 *
Radiation	0.43 ***	0.19 **	0.39 ***	0.12
Min T	-0.22 **	0.14 *	-0.08	-0.22 **
Max T	0.56 ***	0.23 ***	0.50 ***	0.15 *
Min RH	-0.65 ***	-0.15 *	-0.52 ***	-0.25 ***
Max RH	-0.50 ***	-0.00	-0.35 ***	-0.28 ***

B. STRUCTURAL ROOTS

Variables	Correlation Coefficient (r)			
	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.53 ***	-0.18	-0.47 ***	-0.14
Rain	-0.48 ***	-0.29 *	-0.49 ***	0.02
Radiation	0.45 ***	0.19	0.42 ***	0.09
Min T	0.54 ***	-0.09	0.35 **	0.42 ***
Max T	0.59 ***	0.13	0.49 ***	0.22
Min RH	-0.58 ***	-0.13	-0.48 ***	-0.22
Max RH	-0.59 ***	0.02	-0.41 ***	-0.39 ***

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of twenty trees. Lower boles were sampled approximately monthly (11 sampling dates; n=220). Structural roots were sampled every three months (4 sampling dates; n=80).

Table 41. *Dactyladenia barteri*: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficient (r)			
	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.62 ***	-0.29	-0.62 ***	-0.12
Rain	-0.27	-0.37 *	-0.34 *	0.20
Radiation	0.55 ***	0.23	0.54 ***	0.13
Min T	-0.10	-0.09	-0.11	0.01
Max T	0.58 ***	0.26	0.58 ***	0.11
Min RH	-0.58 ***	-0.29	-0.58 ***	-0.09
Max RH	-0.45 **	-0.20	-0.45 **	-0.09

B. STRUCTURAL ROOTS

Variables	Correlation Coefficient (r)			
	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.21	0.34	0.05	-0.42
Rain	-0.23	0.03	-0.13	-0.11
Radiation	0.17	-0.32	-0.07	0.40
Min T	0.20	-0.47	-0.13	0.52 *
Max T	0.24	-0.35	-0.04	0.42
Min RH	-0.24	0.31	0.02	-0.39
Max RH	-0.22	0.49	0.13	-0.56 *

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of four trees. Lower boles were sampled approximately monthly (11 sampling dates; n=44). Structural roots were sampled every three months (4 sampling dates; n=16).

Table 42. *Gliricidia sepium*: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficient (r)			
	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.42 **	0.07	-0.31 *	-0.24
Rain	-0.39 **	-0.19	-0.45 **	0.06
Radiation	0.30 *	-0.13	0.17	0.25
Min T	-0.33 *	0.04	-0.25	-0.16
Max T	0.33 *	0.04	0.30 *	0.10
Min RH	-0.48 ***	-0.06	-0.45 **	-0.13
Max RH	-0.53 ***	-0.01	-0.45 **	-0.20

B. STRUCTURAL ROOTS

Variables	Correlation Coefficient (r)			
	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.63 **	-0.38	-0.62 *	-0.24
Rain	-0.62 *	-0.63 **	-0.79 ***	0.49
Radiation	0.54 *	0.34	0.54 *	-0.28
Min T	0.62 *	0.00	0.34	0.23
Max T	0.70 **	0.36	0.64 **	-0.18
Min RH	-0.70 **	-0.37	-0.65 **	0.17
Max RH	-0.68 **	-0.09	-0.44	-0.13

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of four trees. Lower boles were sampled approximately monthly (11 sampling dates; n=44). Structural roots were sampled every three months (4 sampling dates; n=16).

Table 43. *Leucaena leucocephala*: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficient (r) Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.68 ***	-0.12	-0.61 ***	-0.46 **
Rain	-0.62 ***	0.09	-0.44 **	-0.53 ***
Radiation	0.49 ***	0.20	0.49 ***	0.27
Min T	-0.24	0.45 **	0.05	-0.49 ***
Max T	0.72 ***	0.24	0.70 ***	0.39 **
Min RH	-0.84 ***	-0.01	-0.67 ***	-0.63 ***
Max RH	-0.62 ***	0.24	-0.36 *	-0.64 ***

B. STRUCTURAL ROOTS

Variables	Correlation Coefficient (r) Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.76 ***	-0.42	-0.79 ***	-0.29
Rain	-0.64 **	-0.37	-0.65 **	-0.18
Radiation	0.65 **	0.50 *	0.73 **	0.15
Min T	0.83 ***	-0.09	0.63 **	0.76 ***
Max T	0.85 ***	0.27	0.79 ***	0.46
Min RH	-0.84 ***	-0.21	-0.76 ***	-0.49
Max RH	-0.89 ***	-0.05	-0.74 **	-0.69 **

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of four trees. Lower boles were sampled approximately monthly (11 sampling dates; n=44). Structural roots were sampled every three months (4 sampling dates; n=16).

Table 44. *Pterocarpus soyauxii*: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficients (r)			
	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.76 ***	-0.38 *	-0.80 ***	-0.46 **
Rain	-0.70 ***	-0.15	-0.68 ***	-0.50 ***
Radiation	0.60 ***	0.45 **	0.67 ***	0.29
Min T	-0.25	0.16	-0.18	-0.26
Max T	0.74 ***	0.37 *	0.77 ***	0.43 **
Min RH	-0.85 ***	-0.17	-0.82 ***	-0.62 ***
Max RH	-0.61 ***	0.06	-0.53 ***	-0.52 ***

B. STRUCTURAL ROOTS

Variables	Correlation Coefficients (r)			
	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.83 ***	-0.12	-0.72 **	-0.40
Rain	-0.85 ***	-0.11	-0.73 **	-0.46
Radiation	0.72 **	0.23	0.69 **	0.23
Min T	0.67 **	-0.39	0.33	0.74 **
Max T	0.88 ***	-0.05	0.67 **	0.58 *
Min RH	-0.88 ***	0.09	-0.64 **	-0.63 **
Max RH	-0.77 ***	0.27	-0.47	-0.70 **

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of four trees. Lower boles were sampled approximately monthly (11 sampling dates; n=44). Structural roots were sampled every three months (4 sampling dates; n=16).

Table 45. *Senna siamea*: Correlations between weather variables and reserve carbohydrate concentrations from November, 1991 through November, 1992.

A. LOWER BOLES

Variables[1]	Correlation Coefficient (r)			
	Sugar[2] (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.80 ***	-0.68 ***	-0.82 ***	0.15
Rain	-0.71 ***	-0.37 *	-0.64 ***	-0.16
Radiation	0.59 ***	0.63 ***	0.66 ***	-0.28
Min T	-0.36 *	0.21	-0.17	-0.55 ***
Max T	0.79 ***	0.73 ***	0.84 ***	-0.20
Min RH	-0.94 ***	-0.61 ***	-0.90 ***	-0.07
Max RH	-0.73 ***	-0.24	-0.60 ***	-0.34 *

B. STRUCTURAL ROOTS

Variables	Correlation Coefficient (r)			
	Sugar (mg g^{-1})	Starch (mg g^{-1})	Total CHO (mg g^{-1})	Sugar %
Weather Covariate	-0.69 **	-0.34	-0.71 **	-0.19
Rain	-0.53 *	-0.57 *	-0.67 **	0.15
Radiation	0.58 *	0.22	0.57 *	0.22
Min T	0.85 ***	0.35	0.85 ***	0.28
Max T	0.79 ***	0.44	0.84 ***	0.16
Min RH	-0.79 ***	-0.48	-0.85 ***	-0.11
Max RH	-0.89 ***	-0.36	-0.88 ***	-0.31

[1] Weather variables are sampling-interval means. Weather Covariate = a summary value calculated by principal components analysis; Rain = rainfall (mm); Radiation = solar radiation (W m^{-2}); Min T = minimum temperature (°C); Max T = maximum temperature (°C); Min RH = minimum relative humidity (%); Max RH = maximum relative humidity (%).

[2] Carbohydrate values are based on repeated sampling of four trees. Lower boles were sampled approximately monthly (11 sampling dates; n=44). Structural roots were sampled every three months (4 sampling dates; n=16).

Differences among species can be graphically portrayed by plotting the linear relationships between the carbohydrate variables and weather covariates (such as those included in Tables 41-45) that summarize information provided by the different weather variables. Although regressions of this sort greatly simplify the relationship between weather conditions, phenology, and reserve carbohydrates, they can be helpful in visualizing species differences. Therefore, Figures 22-25 were included in the present study. Starch values were not included because, generally, the linear relationships between starch variables and weather covariates were not significant. In Figures 22-25, the weather covariate refers to a weather continuum with conditions of higher moisture, lower temperature, and less solar radiation on the high end of the scale, and conditions of lower moisture, higher temperature, and more solar radiation on the low end.

Bole sugar (Figure 22) and root sugar (Figure 23) in each species decreased as the weather covariate increased. As indicated by the slopes of the regression lines, the decrease was more drastic in leucaena, *P. soyauxii*, and *S. siamea* than in gliricidia and *D. barteri*. Slopes were compared for significant differences ($P \leq 0.05$). In boles, the former three species were significantly different from the latter two species. In roots, the slopes of leucaena,

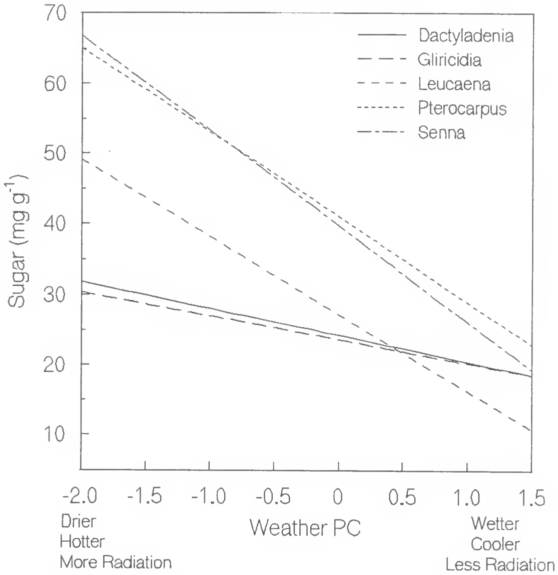

Figure 22. Sugar concentrations in the lower boles of five tree species, as affected by weather. Weather PC is a value—calculated with principal components analysis—that consolidates the different weather variables.

Dactyladenia barteri:	Y = 24.3 - 3.8 X	(r = -.62***)	a
Gliricidia sepium:	Y = 23.6 - 3.4 X	(r = -.42**)	a
Leucaena leucocephala:	Y = 27.2 - 11.0 X	(r = -.68***)	b
Pterocarpus soyauxii:	Y = 41.0 - 12.1 X	(r = -.76***)	b
Senna siamea:	Y = 39.7 - 13.6 X	(r = -.80***)	b

Regression equations that are followed by the same letter have slopes that are not significantly different at the 5% level.

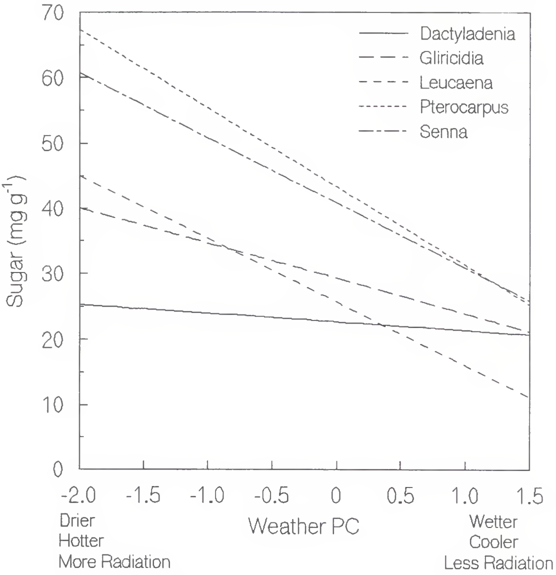

Figure 23. Sugar concentrations in the structural roots of five tree species, as affected by weather. Weather PC is a value—calculated with principal components analysis—that consolidates the different weather variables.

Dactyladenia barteri:	Y = 22.7 - 1.3 X	(r = -.21)	a
Gliricidia sepium:	Y = 29.3 - 5.4 X	(r = -.63**)	ab
Leucaena leucocephala:	Y = 25.7 - 9.7 X	(r = -.76***)	bc
Senna siamea:	Y = 40.9 - 10.0 X	(r = -.69**)	bc
Pterocarpus soyauxii:	Y = 43.4 - 12.0 X	(r = -.83***)	c

Regression equations that are followed by the same letter have slopes that are not significantly different at the 5% level.

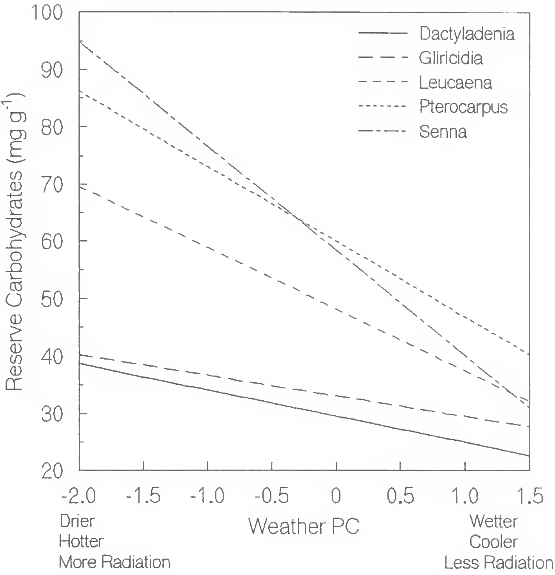

Figure 24. Total reserve carbohydrate concentrations in the lower boles of five tree species, as affected by weather. Weather PC is a value—calculated with principal components analysis—that consolidates the different weather variables.

Dactyladenia barteri:	Y = 29.5 - 4.6 X	(r = -.62***)	a
Gliricidia sepium:	Y = 33.1 - 3.6 X	(r = -.31*)	a
Leucaena leucocephala:	Y = 48.2 - 10.7 X	(r = -.61***)	b
Pterocarpus soyauxii:	Y = 60.0 - 13.1 X	(r = -.80***)	b
Senna siamea:	Y = 58.4 - 18.3 X	(r = -.82***)	c

Regression equations that are followed by the same letter have slopes that are not significantly different at the 5% level.

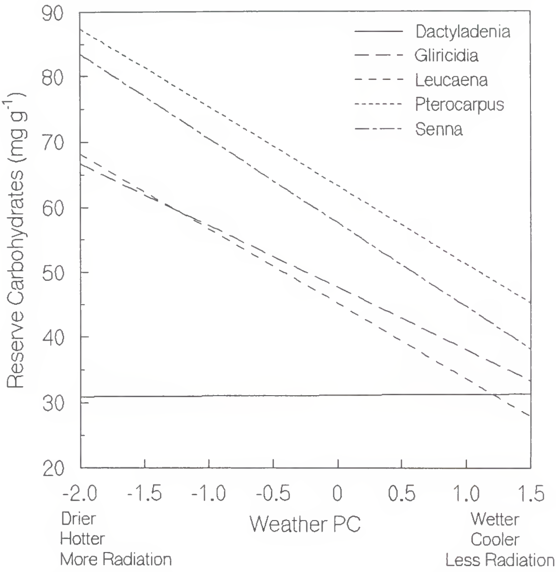

Figure 25. Total reserve carbohydrate concentrations in the structural roots of five tree species, as affected by weather. Weather PC is a value—calculated with principal components analysis—that consolidates the different weather variables.

Dactyladenia barteri:	$Y = 31.2 + 0.1\ X$	($r = .05$)	a
Gliricidia sepium:	$Y = 47.6 - 9.6\ X$	($r = -.62$*)	b
Leucaena leucocephala:	$Y = 45.2 - 11.5\ X$	($r = -.79$***)	b
Pterocarpus soyauxii:	$Y = 63.3 - 12.1\ X$	($r = -.72$**)	b
Senna siamea:	$Y = 57.6 - 12.9\ X$	($r = -.71$**)	b

Regression equations that are followed by the same letter have slopes that are not significantly different at the 5% level.

S. siamea, and *P. soyauxii* were significantly different from that of *D. barteri*, and the slope of *P. soyauxii* was also significantly different from that of gliricidia.

For all species, total reserve carbohydrates in boles decreased as the weather covariate increased (Figure 24). Decline was greatest in *S. siamea*, followed by leucaena and *P. soyauxii*. Gliricidia and *D. barteri* showed the least response. Differences between these three groups of species were significant. In roots, total reserve carbohydrates in *D. barteri* increased slightly as the weather covariate increased, but in all other species total reserve carbohydrates decreased (Figure 25). The slope of *D. barteri* was significantly different from those of the other species.

Phenology and Reserve Carbohydrate Concentrations

The timing of many plant processes is dependent on environmental cues. Therefore, when considering reserve carbohydrate trends, the effects of weather and a plant's growth stage must be considered together. In this section, the phenology of each species, as observed during the study period, will be described in relation to reserve carbohydrate trends in the lower boles of trees. Figures 17-21 provide information on phenological stages, reserve carbohydrate concentrations in boles, and weather during the study period.

Dactyladenia barteri

In this species, flower production started in October, reached a peak from mid-November through December, and tapered off in January. Fruit production started towards the end of December and reached its peak from February through mid-March. By late April, most fruits had ripened and fallen from the trees. Trees retained leaves throughout the year. New foliage and shoot growth were observed in every month except February and March (Figure 17).

Sugar, starch, and total reserve carbohydrate levels were at their highest during the dry season (Figure 17, Table 35). Sugar and total reserve carbohydrates increased steadily in the first half of the dry season, while trees were in the flowering phase. Starch also reached its peak during this period. In contrast, all reserve carbohydrates decreased during the fruit maturation phase (March 17 sampling date). After fruit production ended, sugar and total reserve carbohydrates climbed to the highest levels observed during the study period. From the peak in April, reserve carbohydrates progressively decreased until reaching their lowest levels in October. During this period of gradual decline, shoot and leaf production was constant.

Gliricidia sepium

In gliricidia, flowering took place in December and January, and fruit production from December through February. Trees began to shed leaves in November, at the

beginning of the dry season. By January and February, crowns were sparse or bare. New leaf production started towards the end of February, and coincided with the last part of the fruit production phase. By early April, crowns were full. Leaf and shoot growth continued through June, but on the July 27 sampling date, leaf yellowing and abscission were observed on most trees in the gliricidia plot. This continued during the next two months, leaving many crowns sparse. In October, new leaf growth was observed, and by November crowns were slightly more dense (Figure 18).

Leaf loss during the period from July through October may have been associated with stress among the trees in the gliricidia plot. No leaf loss during this period was observed in the control plots of the cutting frequency experiment (Chapter 3). Several gliricidia trees in the arboretum plot also produced a few out-of-season flowers while leaf loss was occurring. This is often an indication of stress. Additionally, in December 1992 (after sampling ended), it was observed that some structural roots had flaking bark and dry wood. Given the possibility that stress may have affected carbohydrate cycles in the arboretum's gliricidia trees, data from control trees in the cutting frequency experiment are included for comparison in the following discussion.

Sugar in the lower boles of arboretum trees increased from the beginning of the dry season to a peak in January (Figure 18, Table 36). During this time, trees shed leaves, flowered, and began fruit production. Sugar levels decreased between January 24 and March 22 as fruit ripened and new leaf production began. Sugar levels remained fairly consistent during the subsequent seven sampling periods, although they decreased slightly from June through November when leaf loss was observed. The two months with the lowest sugar levels were November, 1991 (the first sampling date) and November, 1992 (the last sampling date). The similar values obtained on these sampling dates suggest that if trees were experiencing unusual stress during 1992, sugar levels and trends were not affected.

Sugar in the stems of control trees in the cutting frequency experiment followed the same general trend that was observed in the arboretum trees. Sugar concentrations in the boles of the arboretum and control trees were also similar (Figure 2). The main difference between trees from the two sites was that dry-season sugar levels remained high much longer in the control trees. In the arboretum trees, sugar levels began to decrease after January 15, during the second half of the dry season. In the control trees, the decrease occurred after April 30, one month after the rains had begun. Fruit production and regrowth of foliage were completed long before the decrease occurred.

In a comparison of stem and root trends in the control trees, it was found that dry-season sugar levels increased later in roots than in stems (January 15 versus December 2 sampling date), and decreased earlier in roots than in stems (April 30 versus June 16 sampling date) (Figures 2 and 3). As with boles, sugar concentrations in the roots of arboretum and control trees were comparable.

With the exception of an April increase, starch in the lower boles of arboretum trees decreased from November, 1991 through July, 1992. In April, when the increase occurred, crowns were dense with young, fully expanded leaves. From a July 27 low point, starch increased to a November peak. This steady increase coincided with the sugar decrease and period of wet-season leaf-shedding that were described above.

Starch levels in the boles of control trees in the cutting frequency experiment were generally three to four times higher than levels in the arboretum trees (Figure 4). This may be a reflection of stress in the arboretum trees, i.e., photosynthate production may have been inadequate to support high levels of carbohydrate storage. Despite this, the annual trend for starch in the arboretum and control trees was similar. Starch levels in both arboretum and control trees were lowest in June and July, coinciding with the period of greatest leaf production and shoot expansion (May through July). From this low point, starch levels

steadily increased to a November peak in arboretum trees, and a late October peak in the control trees (which were not sampled in November). The starch peaks occurred at the beginning of the dry season, as trees were beginning to shed leaves. After reaching the October/November peak, starch levels began to decrease. In contrast to the arboretum trees, starch in control trees increased to a second peak in January, before beginning the decline to the June/July low point. Additionally, control trees had no April increase in starch.

The decrease in starch that occurred after mid-January in control trees, while sugar levels remained high, suggests that sugar levels were being maintained by starch conversion. It is possible that the January decrease in sugar levels in arboretum trees occurred because starch levels were too low to maintain high sugar concentrations once leaf production resumed.

In the control trees, starch trends in roots were similar to those observed in stems, although there were some differences. Starch in roots peaked later in the dry season than in stems (January versus October), and there was a steady increase from June to January, with no December decrease (Figures 4 and 5). In both stems and roots, starch began to decrease after the January 15 sampling date. Starch levels in roots remained low only during June, while in stems low levels continued through July.

In arboretum trees, root starch decreased throughout the study period and was lowest in October, long after starch had begun to increase in the control trees. Furthermore, starch levels in the roots of arboretum trees were much lower than those in the control trees. In the arboretum trees, mean starch concentrations ranged from 6 mg g^{-1} to 26 mg g^{-1}. In control trees, concentrations ranged from 143 mg g^{-1} to 222 mg g^{-1}.

Leucaena leucocephala

In leucaena, heaviest flowering occurred in November and December, but flowers were also observed from May through October. Only in the dry-season and early wet-season months from January through April were no flowers present. Heaviest fruit production occurred from November to early January, and from May through July. Trees maintained full crowns except from mid-February through March when crowns were sparse, but not bare. New foliage production was observed in mid-March, and trees had dense crowns by early April. Vigorous leaf and shoot production continued from April through mid-November. Leaf production almost stopped during the dry season, but even during December, January, and February, a few new leaves were observed on some trees (Figure 19).

Sugar concentrations in the lower boles were highest during the dry-season months from late December through March (Figure 19, Table 37). In contrast, starch decreased

to one of its lowest levels between December 20 and March 17. Total reserve carbohydrates also dipped at this time. At the beginning of this period (late December and early January), flowering was tapering off or had ceased, and pods were ripening and drying on the trees. From mid-January to mid-March (the period when starch was at its dry-season minimum), little growth was observed. With the approach of the rains, and resumption of active growth, sugar steadily decreased until June. While sugar was decreasing, starch increased to a peak in April and May. At that time, all crowns were full, and a new cycle of flowering and fruiting had just begun. Total reserve carbohydrates peaked in March and April. By June 24, sugar, starch, and total reserve carbohydrates had reached their lowest points. Some flowers were present on trees, pods were ripening, and vigorous leaf and shoot growth were occurring. Sugar, starch, and total reserve carbohydrates increased slightly at the end of July (start of the short dry season), decreased slightly by the end of August, then began to increase again. During the period of heaviest flower and fruit production (November and December), sugar and total reserve carbohydrates continued to increase, while starch levels remained steady.

Pterocarpus soyauxii

P. soyauxii trees in the IITA arboretum produced flowers in January and February, and fruit from February to early April. Fruit load was light in the sampled trees.

Leaves were shed in January and immediately replaced. Except for this dry-season activity, crowns were always dense. Leaf and shoot growth occurred throughout the year, although growth seemed to slow in the dry season, starting in November. Starting in July and continuing until October, insects attacked the new foliage, producing numerous holes in most leaves (Figure 20).

Sugar and total reserve carbohydrate concentrations in lower boles were highest during the dry season (December to April) (Figure 20, Table 38). During that period, trees flowered, produced fruit, shed leaves, and refoliated. Sugar and total reserve carbohydrate levels began to decrease at the end of the dry season, and dropped steadily until late July. In August, there was a slight increase in sugar, and a somewhat larger increase in total reserve carbohydrates. In October, sugar decreased to its lowest level during the study period, and total reserve carbohydrates decreased once more to the July level. The low point for sugar occurred during the period of insect attack. Between October 5 and November 11, sugar and total reserve carbohydrates began their dry-season increase. By this time, the insect attack had ended, and leaf and shoot growth had slowed.

Starch concentrations in the lower boles of *P. soyauxii* were relatively consistent from November to June, although there was a slight decrease in December and January, and a

slight increase in June (Figure 20, Table 38). In July, starch dropped to its lowest level. This occurred during a period of vigorous leaf and shoot growth, and at the beginning of the insect attack. Starch then increased steadily to a November, 1992 peak.

Senna siamea

In this species, flowers were present for much of the year. The heaviest period for flower production was from April through August. In October, November, December (the beginning of the dry season) and March (the end of the dry season) flowers were few and scattered. No flowers were observed in January and February. Fruit production started in April, and was heaviest from May through August. Starting in June, branches with a heavy fruit load, in the tops of crowns, shed their leaves and remained bare for the rest of the study period. Most pods were dry or drying from October onwards. Production of leaves and shoots was observed in most months, but almost stopped during January and February. Trees maintained full crowns throughout the year (Figure 21).

Sugar and total reserve carbohydrate levels increased from November to March (the dry season), decreased from March to July, then leveled off from July through November (Figure 21, Table 39). Starch levels showed almost the same trend, with the difference that starch decreased in January, and then—while sugar was decreasing—increased to an April

peak. It then decreased and leveled off. Sugar and total reserve carbohydrate levels were highest when little active growth was observed. Starch levels peaked as flowering, fruiting, and shoot and leaf production resumed after the dry season. With the resumption of active growth, all reserve carbohydrates decreased, and were then maintained at consistent levels.

Discussion

Mean Reserve Carbohydrate Concentrations

Carbohydrate concentrations reported for woody plants are influenced by the tissue sampled, methodological differences, plant age, season and phenological condition of plants at the time of sampling, and whether data are based on one sample period or annual means. The Literature Review (p. 9) provides values reported for a number of tropical and temperate trees.

The carbohydrate concentrations in the multipurpose trees included in this study—both arboretum trees and control trees in the cutting frequency experiment—were within the range reported for woody species in other studies. In the lower boles of arboretum trees (sampled eleven times during the year), mean carbohydrate concentrations in the five species ranged from 24-40 mg g^{-1} for sugar, 5-23 mg g^{-1} for starch, and 28-58 mg g^{-1} for total

reserve carbohydrates. Concentrations in large roots (sampled four times during the year) ranged from 24-42 mg g^{-1} for sugar, 9-23 mg g^{-1} for starch, and 33-65 mg g^{-1} for total reserve carbohydrates. The lowest values were recorded for *Dactyladenia barteri*, followed by gliricidia, and then by the other three species (Tables 1, 16, 33).

Carbohydrate concentrations in leucaena control trees in the cutting frequency experiment were similar to those in the arboretum trees (Tables 19 and 37). In gliricidia, however, starch levels in the control trees and arboretum trees were much different (Tables 4 and 36). In control trees, stem starch was 39 mg g^{-1} and root starch was 158 mg g^{-1}; in arboretum trees, stem starch was 8 mg g^{-1} and root starch was 16 mg g^{-1}. As noted in the Results section, gliricidia trees in the arboretum seemed to be under stress. They experienced leaf fall during the growing season, produced a few flowers at that time, and at the end of the study period some roots had flaking bark and dry wood. This stress might have reduced photosynthesis to the point of current photosynthate being inadequate to meet plant needs, thereby necessitating the hydrolysis of starch stores.

Annual Trends in Reserve Carbohydrate Concentrations

Reserve carbohydrate values from all five species were combined in an attempt to identify general trends that might apply to multipurpose trees in the seasonally dry tropics

(Table 34, Figure 16). Because lower boles were sampled approximately monthly, the trends were derived mainly from these data. Roots, based on four sample dates, seemed to follow the same or similar trends. Concurrent trends for roots and boles were also reported by McLaughlin et al. (1980) for starch in *Quercus alba*. The following trends were observed in the arboretum trees:

(1) Sugar concentrations were highest during the second half of the long dry season (January - March) and lowest during the second half of the rainy season and the beginning of the long dry season (July - November).

(2) Starch concentrations were highest at the beginning of the rainy season (April - May), but were not significantly lower during the early dry season (November - December). There was a decrease in starch from January through March that coincided with the peak sugar values. The lowest starch concentrations succeeded the April-May maxima and continued for four months (June through early October).

(3) Total reserve carbohydrate concentrations were highest during the dry season and the beginning of the rainy season (December - April). During this period, total reserve carbohydrate values were very consistent from month to month, but proportions of starch and sugar varied. The lowest total reserve carbohydrate concentrations occurred during the second half of the

rainy season (July - October).

These results conform to the predicted trend. As detailed in the Literature Review (Chapter 2, p. 11), numerous studies in temperate areas have reported definite cycles in reserve carbohydrates in woody plants. Concentrations are high during the winter dormant season, but decrease when growth resumes in spring. After vegetative growth slows or stops, concentrations begin to rise again. The few studies that have examined reserve carbohydrate cycles of trees in the seasonally dry tropics have found a similar trend (Olofinboba, 1969; Morales et al., 1992; Erdmann et al., 1993). Carbohydrate concentrations are highest during the dry season, decrease as growth resumes with the onset of the rainy season, and increase again early in the dry season. This was the trend observed in the present study.

In many temperate woody species, there are two seasonal maxima of starch, one in early autumn and the other in spring (Kramer & Kozlowski, 1979). Following the spring maximum, starch decreases as it is used to produce new growth. Following the autumn maximum, it is converted to soluble sugars as part of the cold-hardening process.

An similar trend seems to occur in the seasonally dry tropics. Figure 16 shows two starch maxima, one in the first half of the dry season and one at the beginning of the rainy season. As noted above, a decrease in starch was

observed during the second half of the dry season when sugar concentrations were at their peak. Reproductive growth might have contributed to this decrease in some species, but it is likely that the conversion of starch to sugars as trees developed drought tolerance also contributed.

It has been known since the early part of this century that water deficit often causes a decrease in starch content and sometimes an increase in sugar (Kramer, 1983). A number of studies (reviewed by Geiger and Servaites, 1991) have found that one of the ways in which plants acclimate to drought stress is by the development of dehydration tolerance. Plants that acclimate in this way allocate carbon to form osmotic agents (including soluble carbohydrates) that help tissues endure low water status, maintain turgor, and promote water uptake.

Both starch and sugar were at their maxima during the dry season. Therefore, even if starch hydrolysis occurred, it would not completely explain the high dry-season levels of carbohydrates. Cessation or slowing of active growth played an important role. Each woody plant is a highly integrated system of competing carbohydrate sinks (utilization sites) (Kozlowski, 1992). As the growth rate of different tissues decreases, the strength of the carbohydrate sink decreases as well. This frees carbohydrates for other uses, including storage.

Bradford and Hsiao (1982) observed that droughts, not completely inhibitory to photosynthesis, may inhibit shoot growth, and through reallocation of photosynthates, actually increase carbohydrate stores. Mooney and Chu (1974) reported that an evergreen shrub in the Mediterranean-climate region of California was able to maintain carbon gain throughout the year, although the gain was somewhat reduced by drought. Most carbohydrate storage in that shrub occurred during the dry period. These observations may have applicability in the present study because only gliricidia was completely leafless during the dry season. The other species may have been able to continue some level of photosynthesis.

Effect of Weather and Phenology on Reserve Carbohydrate Concentrations

In field-grown trees, it is not truly possible to separate the effects of weather and phenology when considering reserve carbohydrate levels. Many plant processes are cued by seasonally changing weather conditions. Therefore, a decrease in rainfall might be positively correlated with carbohydrate levels, but a decreasing growth rate would be the factor directly responsible for changes in a tree's carbohydrate concentrations. Nonetheless, linear correlations between reserve carbohydrate levels and several weather variables were evaluated in this study.

Weather. As would be expected from the large difference between dry-season and wet-season concentrations, sugar had the strongest correlations with weather variables. When all species were considered together, significant correlations were found between sugar and all weather variables—rainfall, temperature, relative humidity, and radiation (Table 40). The strongest correlations were with minimum relative humidity (r=0.65) and maximum temperature (r=0.56). Correlations with starch were much lower than for sugar, although several were significant. The strongest correlation was with maximum temperature (r=0.23). Judging from Figure 16, a more complex relationship—linked to phenology and changes in sugar levels—is required to describe starch cycles during the year. For example, starch first increased then decreased during the dry season, and repeated that trend during the wet season.

To obtain an indication of differences among the five species regarding their response to weather, the carbohydrate variables for each species were regressed against principal components covariates that summarized the different weather variables (Figures 22-25). Regression coefficients (slopes) were then compared for significant differences at the 5% level. Although these graphs greatly simplified the relationship between weather and reserve carbohydrates, they allowed species comparisons, except for starch. The general lack of significant correlations

between starch and the weather covariate prevented species comparisons for this carbohydrate. Based on steepness of slope, sugar and total reserve carbohydrate concentrations in *Dactyladenia barteri* and gliricidia were generally less affected by weather than were those in the other species.

Phenology. The most obvious trend observed in this study was the inverse relationship between reserve carbohydrate levels and the amount of active growth. During the dry season, when little growth occurred, carbohydrate levels increased to the seasonal maxima. When active growth resumed during the wet season, carbohydrate levels decreased to the seasonal minima (Figures 17-21). As was described in the Literature Review (p. 11), this relationship is well documented, especially in temperate regions.

Figures 17-21 and Tables 35-39 show how reserve carbohydrate concentrations in the different species changed through the year. The lowest starch and total reserve carbohydrate values for most species occurred during June and July, approximately two and one-half to four months after the start of the rainy season. At that time, concentrations were generally 40-50% of the dry-season maxima. In most species, replenishment of starch stores began soon after concentrations reached a minimum. The lowest sugar values occurred later in the year, usually in October and November, although concentrations were fairly consistent from June to November. These findings indicate

that starch and sugar reserves (as well as current photosynthate) were used to support early wet-season growth. After approximately three months, current photosynthesis supplied plant needs, and replenishment of starch stores began. However, because trees continued to produce new shoots—and fruit, in the case of leucaena and *Senna*—for the duration of the rainy season, carbohydrate levels remained relatively low until growth slowed.

A number of researchers have reported that the degree of sprout production after cutting is correlated with reserve carbohydrate concentrations (refer p. 145 for citations). The cutting frequency experiment of the present study (Chapter 3) found evidence that this is true in gliricidia and leucaena. Therefore, if the goal is to maximize and sustain dry matter production, June and July are probably the worst months to cut trees in this region, although the period from August to October is not much better. Carbohydrate values tended to remain low throughout the wet season. In crop-production systems, some tree cutting is inevitable during the wet season in order to minimize the detrimental effects of shading on crop growth. This is probably not as great a problem as it might be with deciduous trees in temperate areas. Many agroforestry trees are capable of producing or retaining leaves during the dry season, and can therefore continue some degree of photosynthesis and carbohydrate replenishment during that

period. Pruned gliricidia and leucaena are capable of producing shoots and foliage even during the dry season.

Kays and Canham (1991) cautioned that trees with an indeterminate growth habit may have a longer period of vulnerability with respect to cutting than do trees with a determinate growth habit. This is true because such trees continue active growth longer, and have a shorter period in which to replenish carbohydrate stores before the dormant season begins. Although, to some extent, this consideration probably applies to the species in the present study, its importance is reduced by the potential of many agroforestry trees for dry-season photosynthesis.

It has been noted that evergreen trees tend to store less carbohydrates than deciduous trees but accumulate them later in the autumn (Kozlowski, 1991). Therefore, seasonal variations in reserve carbohydrate levels are smaller in evergreen than in deciduous trees (Mooney & Hays, 1973; McLaughlin et al., 1980; Kozlowski, 1991). Mooney and Hays (1973) compared the carbohydrate storage cycles in two trees, the drought-deciduous California buckeye (*Aesculus californica*) and the evergreen oak (*Quercus agrifolia*). In buckeye stems, large changes in carbohydrate content occurred through the seasons. During fall fruit production, while trees were leafless, carbohydrate levels fell from more than 17% of dry weight to approximately 10%. When new leaves were produced in February, carbohydrates decreased

further to about 5%, after which concentrations were quickly restored to seasonal highs. In contrast, oak stems experienced very little change in carbohydrate content. Values ranged from approximately 3.5% during fruit production to 5.5% in early spring.

Based on the above observations, it would be expected that *Gliricidia sepium*—the only drought-deciduous species in this study—would have more reserve carbohydrates, more seasonal variation, and earlier accumulation of carbohydrates than the evergreen trees. Evidence to support this is ambiguous, particularly because the gliricidia trees in the arboretum appeared to be stressed, and this may have affected reserve carbohydrate levels and cycles. Table 33 shows that gliricidia did not have higher mean carbohydrate levels than the other species. In fact, they were higher only than those in *Dactyladenia*. In the gliricidia cutting frequency experiment, however, carbohydrate concentrations in control trees were much higher than concentrations in the arboretum species (Table 1). With respect to seasonal variation, the minimum stem starch concentrations in the different species were generally 50 to 60% lower than maximum values. For gliricidia trees in the arboretum this figure was 80% (indicating greater seasonal variation), but for control trees in the cutting frequency experiment it was 55%. Finally, regarding the timing of carbohydrate accumulation, most species began to accumulate stem starch

soon after minimum values occurred in June or July (Figures 17-21). Gliricidia, *Pterocarpus* and *Dactyladenia* all reached maxima in November, while the other species did so in the early part of the rainy season (April-June). Judging from the above results, there seems to be no clear-cut distinction between deciduous gliricidia and the other species.

Recent reviews of reserve carbohydrates in woody species have indicated that nonstructural carbohydrates in all vegetative tissues may be decreased by the presence of reproductive sinks (Loescher et al., 1990; Kozlowski, 1992). However, these reviews also cite studies that have shown equal or higher amounts of nonstructural carbohydrates in tissues of bearing- compared to nonbearing trees. Results from the present study suggest that reproductive growth reduced reserve carbohydrate levels in the lower boles of some study trees.

In *Dactyladenia barteri*, flower production peaked in November and December, while fruit production was heaviest from February to mid-March. During fruit maturation (March 17 sampling date), sugar, starch, and total reserve carbohydrates decreased in the lower boles (Table 35, Figure 17). No shoot growth was observed at that time. After fruit fall, sugar and total reserve carbohydrates increased to their highest levels during the study.

Gliricidia sepium flowered and produced fruit during the dry season, while crowns were bare or sparse. Control trees in the cutting frequency experiment showed no reduction in reserve carbohydrates at this time. However, reproductive growth may have contributed to decreased reserve carbohydrate levels in arboretum trees, which had much lower starch stores than did control trees (Table 36, Figure 18). From the time fruit production began at the end of December until it ended in mid-March, bole starch decreased. In the last part of this period, when fruit maturation was at a peak, sugar levels also dropped sharply. This drop did not occur in control trees, possibly because of their large starch stores. No other growth was taking place when sugar levels decreased, although new shoot production started soon after. These results suggest that reproductive growth will not considerably affect carbohydrate stores in the lower boles of gliricidia unless reserves are already low when reproduction occurs.

In *Leucaena leucocephala*, there were two main periods of fruit production: November to early January, and May to July. There were also two starch minima: January and June (Table 37, Figure 19). The January decrease may have occurred too late to be explained by reproductive growth, but the June decrease occurred when fruit ripening was at a peak. When fruiting ended, both starch and sugar levels increased. Continuous shoot growth occurred before, during,

and after this period so probably was not responsible for the June decrease. In the cutting frequency experiment, reproductive growth was also associated with decreases in starch (see p. 132).

Senna siamea produced flowers and fruit almost continuously from April through December, but fruit load was heaviest from May through August. Except for January and February, active shoot growth continued throughout the year. All carbohydrate levels decreased until June and were then consistent through November (Table 39, Figure 21). Because vegetative and reproductive growth occurred concurrently during the entire period of lowered carbohydrate concentrations, it was not possible to attribute the decrease to one or the other. However, beginning in June, many branches with heavy fruit loads, at the top of tree crowns, were completely bare of foliage. This was probably due to depletion of carbohydrate stores. Carbohydrates are first depleted close to the site of utilization (Kozlowski & Keller, 1966). In a study of coffee (*Coffea arabica*), Cannell (1971) found that starch disappeared from branch wood during rapid fruit expansion. This probably caused considerable movement of carbohydrates from other parts of the tree into the branches.

Pterocarpus soyauxii shed and regrew foliage during January, and produced a light fruit crop in February to April. Neither event seemed to affect reserve carbohydrate

levels in the lower boles of trees (Table 38, Figure 20). However, a decrease in starch concentrations on the July sampling date may have been associated with defoliating insects. Beginning in July and continuing until October, many leaves—especially young leaves—were riddled with holes. As reviewed by Kozlowski (1992), woody plants can produce a variety of secondary compounds from carbohydrates, which provide protection from insect attack. The overall C costs of defense, however, can be high. The starch decrease observed in July may reflect the cost of defense against insect attack.

CHAPTER 5
CONCLUSIONS AND RECOMMENDATIONS

Cutting Frequency and Reserve Carbohydrates

This study found that frequent cutting will decrease concentrations of starch and total reserve carbohydrates (starch + soluble sugars) in the stems and roots of *Gliricidia sepium* and *Leucaena leucocephala*. If frequent cutting is continued for an extended period, it can deplete reserve carbohydrate stores and contribute to tree mortality. However, these two species demonstrated a high tolerance for repeated cutting. Mortality was observed only in leucaena, after twelve cuts.

Response to cutting varies according to species, storage tissue, and season. In both species, starch levels in cut trees decreased first in stems, and after additional cuts, in roots. This indicates the importance of stems (or stumps) for the growth of coppice sprouts. Dry-season cuts had little definite effect on carbohydrate levels in gliricidia, but stem starch in leucaena was quickly decreased by cutting during the dry season. Cutting during the wet season, when growth was more rapid, decreased carbohydrate levels more quickly. Nevertheless, when gliricidia was cut at the end of the dry season, root starch

levels were little affected despite vigorous regrowth. Additional cuts were needed to significantly decrease root starch concentrations.

In these species, no starch replenishment occurred during the first six weeks after cutting. This was demonstrated by the similar reserve carbohydrate concentrations in the 6-week and 3-week treatments. Any photosynthate produced during this period apparently was used for shoot growth.

The species differed in the time required for replenishment of carbohydrate stores. Following a cut at the end of the dry season, starch stores in leucaena stems and roots were substantially restored after three months. In gliricidia, stem starch began recovery within three months but after seven months, levels were still only 50% those in control trees. However, as noted above, root starch in gliricidia was little affected by this cut, so required no replenishment.

Cutting can delay replenishment of carbohydrate stores. In gliricidia, trees in the control and seasonally cut treatment began starch replenishment soon after minimum levels were reached in June or July. In the two frequently cut treatments, no increase in root starch was observed until four months later, in October. Starch levels in the stems remained low in these two treatments, but perhaps an increase occurred after sampling ended. If so, this would

affect estimates of time required for replenishment. The fact that starch levels increased in gliricidia roots, even after frequent cutting during the preceding ten months, demonstrates the importance of these stores.

Dry Matter Production

Frequent cutting reduced dry matter production in gliricidia and leucaena. The seasonally cut treatment produced much more dry matter than the 6-week treatment, which produced much more dry matter than the 3-week treatment. The 6-week and 3-week treatments had similar reserve carbohydrate concentrations, so carbohydrate differences did not account for the higher productivity in the 6-week treatment. Rather, this was due to the greater amount of time trees in the 6-week treatment spent in the linear growth phase.

During the last growth interval, when trees in both the 6-week and 3-week treatments were allowed to grow for six weeks, the 3-week treatment actually produced significantly more biomass than the 6-week treatment. This suggests that some factor in the more frequently cut treatment—perhaps higher levels of growth regulators—contributed to quick regrowth.

Dry matter production increased dramatically with the onset of the rainy season. For example, in gliricidia's 6-week treatment, biomass production increased more than

five times from the last dry-season harvest date to the first wet-season harvest date. The same treatment in leucaena experienced an increase of more than two times. It was speculated that the greater production in gliricidia was due to larger stores of stem starch.

As the length of the cutting interval increased, the proportion of stems to leaves increased. Although stems in the 6-week and 3-week treatments were generally green and succulent, longer growth periods produced more wood. This has important management implications. Cutting intervals can be modified based on the desired output, e.g., mulch, fodder, poles, fuelwood, or timber.

A number of researchers have indicated that low levels of reserve carbohydrates contribute to poor coppice growth. Results of the present study provide additional support for this idea. A number of significant correlations were found between dry matter production and concentrations of the different carbohydrate variables. In both gliricidia and leucaena, there generally were strong positive correlations between dry matter, and stem and root starch levels.

Seasonal Trends in Reserve Carbohydrates

Definite seasonal trends in reserve carbohydrates were observed in the five species of multipurpose trees that were included in this study. Concentrations of sugar and total reserve carbohydrates were highest during the dry season.

Starch had two maxima, one early in the dry season, and one early in the wet season. Starch levels decreased somewhat during the intervening months, when sugar levels were at a peak. This suggests the conversion of starch to sugar as trees developed drought tolerance.

All carbohydrate values decreased as active growth resumed during the wet season. The lowest starch and total reserve carbohydrate levels generally occurred in June or July, two and one-half to four months after the rains commenced. Slow replenishment began soon after. Sugar concentrations reached minimum levels in October and November. In general, all carbohydrate values were relatively low from June to October, as active growth continued. They increased only when dry weather slowed growth.

In several species, carbohydrate concentrations in the lower boles decreased during reproductive growth. The decrease was greatest during the last phase of fruit maturation.

Management Considerations

The management of agroforestry trees must be integrated into the larger framework of farm resources and objectives. Therefore, it is not possible to delineate a specific management strategy that will suit all situations. The timing of cuts will probably be determined by crop needs,

labor availability, and the type of product preferred, e.g. fodder, green mulch, or poles. Nevertheless, an understanding of the biological factors that influence tree growth can provide useful guidelines.

This study has examined reserve carbohydrates in an attempt to identify the best times, from a biological perspective, to cut trees. Several points are evident.

- Too frequent cutting (e.g., every six weeks) will decrease, and eventually deplete, reserve carbohydrates. This will decrease biomass production and contribute to tree mortality. A longer cutting interval should be used.
- Complete replenishment of reserve carbohydrates varies by species, but will probably require a minimum of three months. This might be a good rule-of-thumb recommendation for minimum cutting interval.
- Gliricidia, leucaena, and other alley-cropping trees have shown a remarkable tolerance for frequent cutting. Cutting intervals that are too short for complete carbohydrate replenishment may progressively reduce biomass production, but unless continued for long periods, probably will not kill well-established trees. Trees subjected to this type of management would benefit from occasional fallow "recovery" periods in which to rebuild carbohydrate reserves.
- The use of reserve carbohydrate concentrations to predict cutting tolerance or sprouting ability may be of some use

when evaluating trees of the same species, but is of little use for comparing species. In this study, gliricidia had much larger starch reserves than leucaena, but both species were productive and tolerated frequent cutting. Leucaena's reserves were depleted sooner than gliricidia's, but this required more-frequent cuts than would likely occur in a farm setting. Furthermore, leucaena seemed to replenish stores more quickly than gliricidia. It must also be cautioned that the level of carbohydrate reserves is only one of many interacting factors that influence coppice production.

- The best times to cut are when carbohydrate reserves are high and when cutting will least affect carbohydrate levels. The arboretum experiment showed that carbohydrate concentrations are highest during the dry season. The cutting frequency experiment showed that dry-season cuts will probably have a lesser impact on reserve carbohydrates than wet-season cuts. Therefore, the dry season is the best time to cut.
- The worst time to cut is when reserve carbohydrate levels are low. Minima generally occur near the end of a vigorous growth phase, whether vegetative growth or reproductive growth. In the IITA region, the worst time to cut is probably two and one-half to four months after the rains begin. This is when starch and total reserve carbohydrates are lowest. It would be preferable to cut earlier (before

reserves reach a minimum) or later (after reserves begin to recover). If cutting must be done when trees have reproductive growth, it is better to cut during flowering and early fruit development than during later stages or immediately after fruiting ends.

It was noted that reserve carbohydrate levels are relatively low from June to October. Since this is the main cropping season, in most cases, farmers would have no choice but to cut trees sometime during this period. This is probably not as large a problem as it might be with deciduous trees in temperate areas. Dry-season photosynthesis can likely replenish some of the carbohydrate stores.

Research Needs

Although coppice forestry has a long history, our understanding of coppice physiology is incomplete. This is a complex field which involves a variety of dynamic and interacting factors—reserve carbohydrates, growth regulators, water, nutrients. More research is needed to increase our understanding of the physiological variables that influence the success of coppice regeneration.

This study provided a first look at seasonal carbohydrate trends in agroforestry trees in the seasonally dry tropics. There is much more to learn. Trees in other tropical regions have yet to be examined. Single-species

studies, conducted over a range of environmental conditions, would be useful. With more sophisticated equipment and techniques, reserve carbohydrate dynamics could be examined at a finer resolution. Such research would help to define the processes involved in the mobilization of carbohydrate reserves—the environmental or physiological catalysts, and the various carbohydrate interconversions. This information might assist in evaluating and selecting species or varieties with superior sprouting ability.

An area of research well worth investigating is the effect of retaining some leaves or shoots in pruned trees. Several studies have found that pruning reinvigorates photosynthesis in retained leaves. Others have found that starch decrease is lessened when some foliage is retained. Studies on this subject could be initiated quite easily.

GLOSSARY

Alley cropping: an agroforestry system in which food crops are grown in alleys formed by hedgerows of trees or shrubs. Hedgerows are cut when crops are planted and periodically pruned to prevent crop shading.

Bole: the stem or trunk of a tree.

Coppice: a management technique in which trees are cut at or near the base in order to promote the production of sprouts.

Cutlass: a large knife or machete that is used to cut vegetation.

Multipurpose tree: trees or shrubs which are deliberately kept and managed for more than one preferred use, product, and/or service.

Nonstructural carbohydrates: a rather ambiguous term that generally encompasses starch, sugars, and their derivatives, but which may also include hemicelluloses, amino acids, and other soluble compounds.

Prune: in strict terms, this is a tree-management technique in which smaller branches and stems are removed. However, as generally used in agroforestry, this term has taken on a larger meaning. It is used to describe almost any cutting procedure used in hedgerow

management, including complete removal of branches, partial removal of branches, and cutting of trees at a variety of heights above ground level. As used in the present paper, it means cutting at 25 cm above ground level and removal of all branches. The term is used interchangeably with "cut" and "cutting."

Reserve carbohydrates: soluble and insoluble carbohydrates that are accumulated and stored in plants, and which can later be mobilized to support biosynthesis for metabolism and growth.

REFERENCE LIST

Abusrewil, G.S., F.E. Larson, and R. Fritts. 1983. Prestorage and poststorage starch levels in chemically and hand defoliated "Delicious" apple nursery stock. J. Amer. Soc. Hort. Sci. 108: 20-23.

Adams, M.B., H.L. Allen, and C.B. Davey. 1986. Accumulation of starch in roots and foliage of loblolly pine (*Pinus taeda* L.): effects of season, site, and fertilization. Tree Physiol. 2: 35-46.

Ahrens, G.R. 1989. Tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) root dieback: below- and aboveground site occupancy by stump-sprouts in southwest Oregon. M.S. thesis. Oregon State University, Corvallis, Oregon.

Alvim, P.T. 1964. Tree growth periodicity in tropical climates. pp. 479-495 In: M.H. Zimmermann (ed.). Formation of Wood in Forest Trees. Academic Press: New York.

Alvim, P.T. and R. Alvim. 1978. Relation of climate to growth periodicity in tropical trees. pp.445-464 In: P.B. Tomlinson and M.H. Zimmermann (eds.). Tropical Trees as Living Systems. Cambridge Univ. Press: London.

ap Rees, T. 1984. Sucrose metabolism. pp. 53-73 In: D.H. Lewis (ed.), Storage Carbohydrates in Vascular Plants. Cambridge University Press: Cambridge.

Arnold, W.N. 1968. The selection of sucrose as the translocate of higher plants. J. Theoretical Biol. 21: 13-20.

Atta-Krah, A.N. and J.E. Sumberg. 1988. Studies with *Gliricidia sepium* for crop/livestock production systems in West Africa. Agrofor. Syst. 6: 97-118.

Bamber, R.K. and F.R. Humphreys. 1965. Variation in sapwood starch levels in some Australian forest species. Austral. For. 29: 15-23.

Berdowski, J.J.M. and H. Siepel. 1988. Vegetative regeneration of *Calluna vulgaris* at different ages and fertilizer levels. Biological Conservation 2: 85-93.

Birk, E.M. and P.A. Matson. 1986. Site fertility affects seasonal carbon reserves in loblolly pine. Tree Physiol. 2:17-27.

Blake, T.J. 1983. Coppice systems for short rotation intensive forestry: the influence of cultural, seasonal and plant factors. Austral. For. Res. 13: 279-291.

Bonicel,A.G., G. Haddad, and J. Gagnaire. 1987. Seasonal variations of starch and major soluble sugars in the different organs of young poplars. Pl. Physiol. Biochem. 25: 451-459.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75: 1437-1449.

Bradford, K.J. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. pp. 263-324 In: O.L. Lange, P.S. Nobel. C.B. Osmond, and H. Ziegler (eds.), Encycl. Plant Physiol., N.S., vol. 12B Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Springer-Verlag: New York.

Bray, R.A. 1994. Diversity within tropical tree and shrub legumes. pp. 111-119 In: R.C. Gutteridge and H.M. Shelton (eds.), Forage Tree Legumes in Tropical Agriculture. CAB International: Wallingford, U.K.

Brewbaker, J.L. 1987. Leucaena: a multipurpose tree genus for tropical agroforestry. pp. 290-323 In: H.A. Steppler and P.K.R. Nair (eds.), Agroforestry: A Decade of Development. ICRAF: Nairobi.

Brewbaker, J.L., N. Hegde, E.M. Hutton, R.J. Jones, J.B. Lowry, F. Moog, and R. van den Beldt. 1985. Leucaena - Forage Production and Use. NFTA: Hawaii.

Budelman, A. 1987. *Gliricidia sepium* (Jacq.) Walp. in the southern Ivory Coast: production, composition, and decomposition of the leaf biomass. pp. 74-81 In: D. Withington, N. Glover, and J. Brewbaker (eds.) *Gliricidia sepium* (Jacq.) Walp.: Management and Improvement. NFTA: Waimanalo, Hawaii.

Budowski, G. 1987. Living fences in tropical America, a widespread agroforestry practice. pp. 169-178 In: H.L. Gholz (ed.), Agroforestry: Realities, Possibilities and Potentials. Martinus Nijhoff: Dordrecht, The Netherlands.

Bullock, S.H. and J.A. Solis-Magallanes. 1990. Phenology of canopy trees of a deciduous forest in Mexico. Biotropica 22: 22-35.

Burkill, H.M. 1985. The Useful Plants of West Tropical Africa, Edition 2. Volume 1. Royal Botanic Gardens: Kew. 960 pp.

Buwai, M. and M.J. Trlica. 1977. Multiple defoliation effects on herbage yield, vigor, and total nonstructural carbohydrates of five range species. J. Range Mgmt. 30: 164-171.

Cannell, M.G.R. 1971. Changes in the respiration and growth rates of developing fruits of *Coffea arabica* L. J. Hort. Sci. 46: 263-272.

Catchpoole, D.W. and G. Blair. 1990. Forage tree legumes. I. Productivity and N economy of leucaena, gliricidia, calliandra and sesbania and tree/green panic mixtures. Austr. J. Agric. Res. 41: 521-530.

Christensen, P.E. and P.C. Kimber. 1975. Effects of prescribed burning on the flora and fauna of South-west Australian forests. Proc. Ecol. Soc. Austr. 9: 85-106.

Coyne, P.I. and C.W. Cook. 1970. Seasonal carbohydrate reserve cycles in eight desert range species. J. Range Mgmt. 23: 438-444.

Cranswick, A.M., D.A. Rook, and J.A. Zabkiewicz. 1987. Seasonal changes in carbohydrate concentration and composition of different tissue types of *Pinus radiata* trees. New Z. J. For. Sci. 17: 229-245.

Danso, A.A. and P. Morgan. 1993. Alley cropping maize (*Zea mays* var. Jeka) with cassia (*Cassia siamea*) in the Gambia: crop production and soil fertility. Agrofor. Syst. 21: 133-146.

Duguma, B., B.T. Kang, and D.U.U. Okali. 1988. Effect of pruning intensity of three woody leguminous species grown in alley cropping with maize and cowpea on an alfisol, Agroforestry Sys. 6:19-35.

Eissenstat, D.M. and L.W. Duncan. 1992. Root growth and carbohydrate responses in bearing citrus trees following partial canopy removal. Tree Physiol. 10: 245-257.

Eliasson L. 1968. Dependence of root growth on photosynthesis in *Populus tremula*. Physiol. Plant. 21: 806-810.

Ella, A., C. Jacobsen, W.W. Stür, and G. Blair. 1989. Effect of plant density and cutting frequency on the productivity of four tree legumes. Trop. Grasslands 23(1):28-34.

Ella, A., W.W. Stür, G.J. Blair, and C.N. Jacobsen. 1991. Effect of plant density and cutting frequency on the yield of four tree legumes and interplanted *Panicum maximum* cv. Riversdale. Trop. Grassl. 25: 281-286.

Erdmann, T. 1991. Effects of Cutting Frequency and Cutting Height on Reserve Carbohydrates in *Gliricidia sepium* (Jacq.) Walp. MS thesis. University of Florida, Gainesville.

Erdmann, T.K., P.K.R. Nair, and B.T. Kang. 1993. Effects of cutting frequency and cutting height on reserve carbohydrates in *Gliricidia sepium* (Jacq.) Walp. Forest Ecology and Management 57: 45-60.

Ferraris, R. 1979. Productivity of *Leucaena leucocephala* in the wet tropics of North Queensland. Tropic. Grassl. 13: 20-27.

Ford, E.D. and J.D. Deans. 1977. Growth of a Sitka spruce plantation: spatial distribution and seasonal fluctuations of lengths, weights, and carbohydrate concentrations of fine roots. Plant and Soil 47:463-485.

Geiger, G.R. and J.C. Servaites. 1991. Carbon allocation and response to stress. pp. 103-127 In: H.A. Mooney, W.E. Winner, and E.J. Pell (eds.), Response of Plants to Multiple Stresses. Academic Press: San Diego.

Gholz, H. L. and W.P. Cropper. 1991. Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. Can. J. For. Res. 21: 1742-1747.

Gibbs, R.D. 1940. Studies in tree physiology: II. Seasonal changes in the food reserves of field birch (*Betula populifolia* Marsh.). Can. J. Res. C 18: 1-9.

Gregory, R.A. and P.M. Wargo. 1986. Timing of defoliation and its effect on bud development, starch reserves, and sap sugar concentration in sugar maple. Can. J. For. Res. 16:10-17.

Guevarra, A.B., A.S. Whitney, and J.T. Thompson. 1978. Influence of intra-row spacing and cutting regimes on the growth and yield of *Leucaena*. Agronomy J. 70:1033-1037.

Haddad, Y., D. Clair-Maczulajtys, and G. Bory. 1995. Effects of curtain-like pruning on distribution and seasonal patterns of carbohydrate reserves in plane (*Platanus acerifolia* Wild.) trees. Tree Physiol. 15: 135-140.

Hansen, P. 1967. ^{14}C-studies on apple trees III. The influence of season on storage and mobilization of labelled compounds. Physiol. Plant. 20: 1103-1111.

Hansen, P. 1971. ^{14}C-studies on apple trees VII. The early seasonal growth in leaves, flowers and shoots as dependent upon current photosynthates and existing reserves. Physiol. Plant. 25: 469-473.

Hansen, P. 1977. Carbohydrate allocation. pp. 247-255. In: J.J. Landsberg and C.V. Cutting (eds.), Environmental Effects on Crop Physiology. Academic Press: London.

Harrington, M.G. 1989. Gambel oak root response to spring, summer, and fall prescribed burning. J. Range Mgmt. 42: 504-507.

Hughes, C.E. 1987. Biological considerations in designing a seed collection strategy for *Gliricidia sepium* (Jacq.) Walp. (Leguminosae). pp. 174-184 In: *Gliricidia Sepium* (Jacq.) Walp.: Management and Improvement. Proceedings of a workshop held at CATIE, Turrialba, Costa Rica, June, 1987. Nitrogen Fixing Tree Association Special Publication 87-01. NFTA: Waimanalo, Hawaii.

Huxley, P.A. 1983. Phenology of tropical woody perennials and seasonal crops with reference to their management in agroforestry systems. pp. 503-525, In, Plant Research and Agroforestry. ICRAF: Nairobi, Kenya.

Huxley, P.A. and W.A. Van Eck. 1974. Seasonal changes in growth and development of some woody perennials near Kampala, Uganda. J. Ecol. 62:579-592.

International Institute of Tropical Agriculture. 1983. Annual Report. IITA: Ibadan, Nigeria.

Jama, B. 1993. Soil fertility and productivity aspects of alley cropping with *Cassia siamea* and *Leucaena leucocephala* under semiarid conditions in Machakos, Kenya. Ph.D. dissertation. Univ. of Florida, Gainesville.

Johansson. T. 1992. Sprouting of 2- to 5-year-old birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth) in relation to stump height and felling time. For. Ecol. Mgmt. 53: 263-281.

Johnson, R.A. and D.W. Wichern. 1988. Applied Multivariate Statistical Analysis (2nd Ed.). Prentice Hall: Englewood Cliffs, USA.

Jones, M.B. and H.M. Laude. 1960. Relationships between sprouting in chamise and the physiological condition of the plant. J. Range Mgmt. 13: 210-214.

Juo, A.S.R. and B.T. Kang. 1989. Nutrient effects of modification of shifting cultivation in West Africa. pp. 289-300 In: J. Proctor (ed.), Mineral Nutrients in Tropical Forest and Savanna Ecosystems. Blackwell Scientific: London, UK.

Kandiah, S. 1971. Studies on the physiology of pruning tea. 1 - turnover of resources in relation to pruning. Tea Quart. 42: 89-100.

Kandiah, S., D.T. Wettasinghe, and G. Wadasinghe. 1984. Root influence on shoot development in tea (*Camellia sinensis* (L.) O. Kuntze) following shoot pruning. J. Hort. Sci. 59: 581-587.

Kang, B.T. 1987. Nitrogen cycling in multiple cropping systems. pp. 333-348 In: J.R. Wilson (ed.), Advances in Nitrogen Cycling in Agricultural Ecosystems. CAB International: Wallingford, UK.

Kang, B.T. 1993. Alleycropping: Past achievements and future directions. Agrof. Syst. 23: 141-155.

Kang, B.T, L. Reynolds, and A.N. Atta-Krah. 1990. Alley farming. Adv. Agron. 43: 315-359.

Kang, B.T., M. Gichuru, N. Hulugalle, and M.J. Swift. 1991. Soil constraints for sustainable upland crop production in humid and subhumid west Africa. pp. 101-112 In: Soil Constraints on Sustainable Plant Production in the Tropics. Tropical Agriculture Research Center: Tsukuba, Japan.

Kang, B.T., H. Grimme, and T.L. Lawson. 1985. Alley cropping sequentially cropped maize and cowpea with leucaena on a sandy soil in southern Nigeria. Plant and Soil 85: 267-277.

Kang, B.T., G.F. Wilson, and L. Sipkens. 1981. Alley cropping maize (*Zea mays*) and leucaena (*Leucaena leucocephala* Lam) in southern Nigeria. Plant and Soil 63: 165-179.

Kays, J.S. and C.D. Canham. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. For. Sci. 37: 524-539.

Keay, R.W.J. 1989. Trees of Nigeria. Oxford University Press: Oxford, U.K. 476 pp.

Keller, J.D. and W.H. Loescher. 1989. Nonstructural carbohydrate partitioning in perennial parts of sweet cherry. J. Amer. Soc. Hort. Sci. 114: 969-975.

Kile, G.A. 1981. Annual variations in soluble sugars, starch, and total food resources in *Eucalyptus obliqua* roots. For. Sci. 27: 449-454.

Kozlowski, T.T. 1971. Growth and development of trees. Vol. 2. Cambial growth, root growth, and reproductive growth. Academic Press: New York.

Kozlowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. Bot.Rev. 58: 107-222.

Kozlowski, T.T., and T. Keller. 1966. Food relations of woody plants. Bot. Rev. 32(4):293-382.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. The Physiological Ecology of Woody Plants. Academic Press: San Diego.

Kramer, P.J. 1983. Water Relations of Plants. Academic Press: San Diego.

Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press: Orlando, Florida.

Krishnamurthy, K. and M.K. Munegowda. 1982. Effect of cutting and frequency regimes on the herbage yield of leucaena. Leuc. Res. Rep. 3: 31-32.

Lal, R. 1989. Agroforestry systems and soil surface management of a tropical Alfisol: I: Soil moisture and crop yields. Agrofor. Syst. 8: 7-29.

Larbi, A., M.A. Jabbar, A.N. Atta-Krah, and J. Cobbina. 1993. Effect of taking a fodder crop on maize grain yield and soil chemical properties in *Leucaena* and *Gliricidia* alley farming systems in western Nigeria. Exp. Agric. 29: 317-321.

Laude, H.M., M.B. Jones, and W.E. Moon. 1961. Annual variability in indicators of sprouting potential in chamise. J. Range Mgmt. 14: 323-326.

Leege, T.A. and W.O. Hickey. 1971. Sprouting of northern Idaho shrubs after prescribed burning. J. Wildl. Mgmt. 35: 508-515.

Lewis, D.H. 1984. Occurrence and distribution of carbohydrates in vascular plants. pp. 1-52 In: D.H. Lewis (ed.), Storage Carbohydrates in Vascular Plants. Cambridge University Press: Cambridge.

Little, E.L. 1983. Common Fuelwood Crops. Communi-Tech Ass.: Morgantown, West Virginia.

Lockwood, D.W. and D. Sparks. 1978. Translocation of ^{14}C in "Stuart" pecan in the spring following assimilation of $^{14}CO_2$ during the previous growing season. J. Amer. Soc. Hort. Sci. 103: 38-45.

Loescher, W.H., T. McCamant, and J.D. Keller. 1990. Carbohydrate reserves, translocation, and storage in woody plant roots. HortScience 25:274-281.

McCamant, T. 1988. Utilization and transport of storage carbohydrates in sweet cherry. MS Thesis, Washington State Univ., Pullman.

McCready, R.M., J. Guggolz, V. Silviera, and H.S. Owens. 1950. Determination of starch and amylose in vegetables. Anal. Chem. 22(9): 1156-1158.

McLaughlin, S.B., R.K. McConathy, R.L. Barnes, and N.T. Edwards. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). Can. J. For. Res. 10: 379-388.

Menke, J.W. and M.J. Trlica. 1981. Carbohydrate reserve, phenology and growth cycles of nine Colorado range species. J. Range Mgmt. 34:269-277.

Mika, A. 1986. Physiological responses of fruit trees to pruning. Hortic. Rev. 8: 337-378.

Miyanishi, K. and M. Kellman. 1986. The role of nutrient reserves in regrowth of two savannah shrubs. Can. J. Bot. 64:1244-1248.

Mooney, H.A. and C. Chu. 1974. Seasonal carbon allocation in *Heteromeles arbutifolia*, a California shrub. Oecologia 14: 295-306.

Mooney, H.A. and R.I. Hays. 1973. Carbohydrate storage cycles in two California mediterranean-climate trees. Flora 162: 295-304.

Moormann, F.R., R. Lal, and A.S.R. Juo. 1975. The Soils of IITA. IITA Tech. Bull. No. 3, IITA, Ibadan.

Morales, J.B., A. Perez-Jimenez, and F. Chiang. 1992. Fluctuation of starch in wood and bark of trees from the Pacific coast of Mexico. Diversity of Pacific Basin woods in past, present, and future, August 14-16, 1992. Lawaii, Hawaii. IAWA Bull. 13: 241-242.

Murali, K.S. and R. Sukumar. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 94: 114-119.

Murneek, A.E. 1942. Quantitative distribution of nitrogen and carbohydrates in apple trees. Missouri Agr. Exp. Sta. Res. Bull. 348.

Nagarajah, S. and Pethiyagoda, U. 1965. The influence of lungs on carbohydrate reserves and growth of shoots. Tea Quart. 36: 88-102.

Nair, P.K.R. 1990. The prospects for agroforestry in the tropics. Tech.Pap. No. 131. World Bank, Washington, D.C.

Nair, P.K.R. 1993. An Introduction to Agroforestry. Kluwer: Dordrecht, the Netherlands.

National Academy of Sciences. 1979. Tropical Legumes: Resources for the Future. NAS: Washington, D.C.

National Academy of Sciences. 1984. Leucaena: Promising Forage and Tree Crop for the Tropics. 2nd edition. National academy Press: Washington, D.C.

Nguyen, P.V., D.I. Dickmann, K.S. Pregitzer, and R. Hendrick. 1990. Late-season changes in the allocation of starch and sugar to shoots, coarse roots, and fine roots in two hybrid poplar clones. Tree Physiol. 7: 95-105.

Njoku, E. 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. J. Ecol. 51: 617-624.

Ogata, K. 1989. Useful timbers of the tropics. (15) African padauk. Tropical Forestry 15: 50-51.

Okafor, J.C. 1979. Edible indigenous woody plants in the rural economy of the Nigerian forest zone. pp.262-300 In: D.U.U. Okali (ed.), The Nigerian Rainforest Ecosystem. Proceedings of Man and the Biosphere Workshop on the Nigerian Rainforest Ecosystem. University of Ibadan, 24-26 January 1979.

Okigbo, B.N. 1977. Neglected plants of horticultural and nutritional importance in traditional farming systems of tropical Africa. Acta Hort. 53:131-150.

Old, K.M., R. Gibbs, J. Craig, B.J. Meyers, and Z.Q. Yuan. 1990. Effect of drought and defoliation on the susceptibility of eucalypts to cankers caused by *Endothia gyrosa* and *Botryosphaeria ribis*.

Oliveira, C.M. and C.A. Priestley. 1988. Carbohydrate reserves in deciduous fruit trees. Hort. Rev. 10: 403-430.

Olofinboba, M.O. 1969. Seasonal variations in the carbohydrates in the xylem of *Antiaris africana*. Ann. Bot. 33: 339-349.

Osman, A.M. 1981. Effects of cutting interval on the relative dry matter production of four cultivars of leucaena. Leuc. Res. Rep. 2: 33-38.

Palada, M.C., B.T. Kang, and S.L. Claassen. 1992. Effect of alley cropping with *Leucaena leucocephala* and fertilizer application on yield of vegetable crops. Agrofor. Syst. 19: 139-147.

Parker J. 1979. Effects of defoliation and root height above a water table on some red oak metabolites. J. Amer. Soc. Hort. Sci. 104: 417-421.

Parker, J. and D.R. Houston. 1971. Effects of repeated defoliation on root and root collar extractives of sugar maple trees. For. Sci. 17: 91-95.

Parker, J. and R.L. Patton. 1975. Effects of drought and defoliation on some metabolites in roots of black oak seedlings. Can. J. For. Res. 5: 457-463.

Pate, J.S., R.H. Froend, B.J. Bowen, A. Hansen, and J. Kuo. 1990. Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S.W. Australia. Ann. Bot. 65: 585-601.

Phillips-Howard, K.D. 1993. Indirect mineland reclamation on the Jos Plateau, Nigeria: the basis for a viable policy. Land Use Policy 10: 2-15.

Pound, B. and L. Martinez Cairo. 1983. Leucaena: Its Cultivation and Uses. ODA: London, UK.

Priestley, C.A. 1960. Seasonal changes in the carbohydrate resources of some six-year-old apple trees. Ann. Rept. E. Malling Res. Sta. 1959. pp.70-77.

Priestley, C.A. 1962. Carbohydrate Resources Within the Perennial Plant. Commonw. Bur. Horticulture and Plantation Crops, Technical Communication 27. East Malling.

Priestley, C.A. 1963. The carbohydrate resources of young apple trees under four levels of illumination. Ann. Bot. 27: 435-446.

Priestley, C.A. 1964. The location of carbohydrate resources within the apple tree. Proc. XVI Intl. Hort. Congr., 1962. 3: 319-327.

Priestley, C.A. 1970. Carbohydrate storage and utilization. pp. 113-127. In: L.C. Luckwill and C.V. Cutting (eds.), Physiology of Tree Crops. Academic Press: New York.

Quinlan, J.D. 1969. Mobilization of ^{14}C in the spring following autumn assimilation of $^{14}CO_2$ by an apple rootstock. J. Hort. Sci. 44: 107-110.

Rodgers, H.L., M.P. Brakke, and J.J. Ewel. 1995. Shoot damage effects on starch reserves of *Cedrela odorata*. Biotropica 27: 71-77.

Roper, T.R., J.D. Keller, W.H. Loescher, and C.R. Rom. 1988. Photosynthesis and carbohydrate partitioning in sweet cherry: fruiting effects. Physiol. Plant. 72: 42-47.

Rose, R., C.L. Rose, S.K. Omi, K.R. Forrey, D.M. Durall, and W.L. Bigg. 1991. Starch determination by perchloric acid vs. enzymes: evaluating the accuracy and precision of six colorimetric methods. J. Agricultural and Food Chem. 39(1): 2–11.

Ruhigwa, B.A., M.P. Gichuru, B. Mambani, and N.M. Tariah. 1992. Root distribution of *Acioa barteri, Alchornea cordifolia, Cassia siamea*, and *Gmelina arborea* in an acid Ultisol. Agrofor. Syst. 19: 67-78.

Ruhigwa, B.A., M.P. Gichuru, N.M. Tariah, N.O. Isirimah, and D.C. Douglas. 1993. Spatial variability in soil chemical properties under *Dactyladenia barteri, Alchornea cordifolia, Senna siamea*, and *Gmelina arborea* hedgerows on an acid Ultisol. Exp. Agric. 29: 365-372.

Saranpää, P. and W. Höll. 1989. Soluble carbohydrates of *Pinus sylvestris* L. sapwood and heartwood. Trees 3: 138-143.

Satoh, M., P.E. Kriedemann, and B.R. Loveys. 1977. Changes in photosynthetic activity and related processes following decapitation in mulberry trees. Physiol. Plant. 41: 203-210.

Schier G.A. and J.C. Zasada. 1973. Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. Can. J. For. Res. 3: 243-250.

Selvendran, R.R. and S. Selvendran. 1972. Changes in the polysaccharides of the tea plant during post-prune growth. Phytochemistry 11: 3167-3171.

Sennerby-Forsse, L., A. Ferm, and A. Kauppi. 1992. Coppicing ability and sustainability. pp. 146-184 In: C.P. Mitchell, J.B. Ford-Robertson, T. Hinckley, and L. Sennerby-Forsse (eds.), Ecophysiology of Short Rotation Forest Crops. Elsevier Applied Science: New York.

Shelton, H.M. and J.L. Brewbaker. 1994. *Leucaena leucocephala* - the most widely used forage tree legume. pp. 15-29 In: R.C. Gutteridge and H.M. Shelton (eds.), Forage Tree Legumes in Tropical Agriculture. CAB International: Wallingford, U.K.

Simons, A.J. and J.L. Stewart. 1994. *Gliricidia sepium* - a multipurpose forage tree legume. pp. 30-48 In: R.C. Gutteridge and H.M. Shelton (eds.), Forage Tree Legumes in Tropical Agriculture. CAB International: Wallingford, U.K.

Singh, K.P. and S.K. Srivastava. 1986. Seasonal variation in the biomass and non-structural carbohydrate content of fine roots of teak (*Tectona grandis L. f.*) plantations in a dry tropical region. Tree Physiol. 1: 31-36.

Sleigh P.A., H.A. Collin, and K. Hardwick. 1984. Distribution of assimilate during the flush cycle of growth in *Theobroma cacao* L. Pl. Growth Regul. 2: 381-391.

SAS Institute. 1988. SAS\STAT User's Guide, Release 6.03 Edition. SAS Institute: Cary, North Carolina. 1028 pp.

Strong, T. 1989. Rotation length and repeated harvesting influence *Populus* coppice production. U.S. For. Serv. Res. Note NC-350.

Stür, W.W., H.M. Shelton, and R.C. Gutteridge. 1994. Defoliation management of forage tree legumes. pp. 158-167 In: R.C. Gutteridge and H.M. Shelton (eds.), Forage Tree Legumes in Tropical Agriculture. CAB International: Wallingford, U.K.

Taylor, J.S., T.J. Blake, and R.P. Pharis. 1982. The role of plant hormones and carbohydrates in the growth and survival of coppiced *Eucalyptus* seedlings. Physiol. Plant. 55: 421-430.

Tew, R.K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. For. Sci. 16: 318-320.

Tian, G., B.T. Kang, and L. Brussaard. 1993. Mulching effect of plant residues with chemically contrasting compositions on maize growth and nutrients accumulation. Plant and Soil 153: 179-187.

Trlica, M.J. and C.W. Cook. 1971. Defoliation effects on carbohydrate reserves of desert species. J. Range Mgmt. 24:418-425.

Tromp, J. 1983. Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. Plant and Soil 71:401-413.

Tschaplinski, T.J. and T.J. Blake. 1989. Photosynthetic reinvigoration of leaves following shoot decapitation and accelerated growth of coppice shoots. Physiol. Plant. 75: 157-165.

Tschaplinski, T.J. and T.J. Blake. 1994. Carbohydrate mobilization following shoot defoliation and decapitation in hybrid poplar. Tree Physiol. 14: 141-151.

van der Meersch, M.K., R. Merckx, K. Mulongoy, and M.K. Van der Meersch. 1993. Evolution of plant biomass and nutrient content in relation to soil fertility changes in two alley cropping systems. pp. 143-154 In: K. Mulongoy and R. Merckx (eds.), Soil Organic Matter Dynamics and the Sustainability of Tropical Agriculture. Proceedings of an International Symposium, Leuven, Belgium, 4-6 November 1991. John Wiley & Sons: Chichester, UK.

Wareing, P.F., M.M. Khalifa, and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220: 453-457.

Wargo, P.M. 1976. Variation of starch content among and within roots of red and white oak trees. For. Sci. 22: 468-471.

Wargo, P.M. 1979. Starch storage and radial growth in woody roots of sugar maple. Can. J. For. Res. 9: 49-56.

Wargo, P.M., J. Parker, and D.R. Houston. 1972. Starch content in roots of defoliated sugar maple. For. Sci. 18: 203-204.

Webb, W.L. and J.J. Karchesy. 1977. Starch content of Douglas-fir defoliated by tussock moth. Can. J. For. Res. 7: 186-188.

Wenger, K.F. 1953. The sprouting of sweetgum in relation to season of cutting and carbohydrate content. Plant Physiol. 28: 35-49.

Whiley, A.W., T.S. Rasmussen, J.B. Saranah, and B.N. Wolstenholme. 1989. Effect of temperature on growth, dry matter production, and starch accumulation in ten mango (*Mangifera indica* L.) cultivars. J. Hort. Sci. 64: 753-765.

White, A.S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. Ecology 64: 1081-1085.

Worley, R.E. 1979. Fall defoliation date and seasonal carbohydrate concentration of pecan wood tissue. J. Amer. Soc. Hort. Sci. 104: 195-199.

Wright, H.A. and K.J. Stinson. 1970. Response of mesquite to season of top removal. J. Range Mgmt. 23:127-128.

Wright, S.J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. Ecology 72: 1643-1657.

Wright, S.J. and C.P. Van Schaik. 1994. Light and the phenology of tropical trees. Amer. Naturalist 143: 192-199.

Yamashita, T. 1986. Mobilization of carbohydrates, amino acids and adenine nucleotides in hardwood stems during regrowth after partial shoot harvest in mulberry trees (*Morus alba* L.). Ann. Bot. 57: 237-244.

Yamashita, T. 1990. Variations in amounts of carbohydrates, amino acids, and adenine nucleotides in mulberry tree (*Morus alba* L.) stems during transitional phases of growth. Tree Physiol. 6: 191-200.

Yamoah, C.F., A.A. Agboola, and K. Mulongoy. 1986a. Decomposition, nitrogen release and weed control by prunings of selected alley cropping shrubs. Agrofor. Syst. 4: 239-246.

Yamoah, C.F., A.A. Agboola, and G.F. Wilson. 1986b. Nutrient competition and maize performance in alley cropping systems. Agrofor. Syst. 4: 247-254.

Yamoah, C.F., A.A. Agboola, G.F. Wilson, and K. Mulongoy. 1986c. Soil properties as affected by the use of leguminous shrubs for alley cropping with maize. Agriculture, Ecosystems and Environment 18: 167-177.

Yemm, E.W. and A.J. Willis. 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57: 508-514.

Young, A. 1989. Agroforestry for Soil Conservation. CAB International: Wallingford, UK. 276 pp.

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